

DEVELOPMENT OF TROPICAL FOREST EDGE VEGETATION

By

GUADALUPE WILLIAMS-LINERA

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL  
OF THE UNIVERSITY OF FLORIDA IN  
PARTIAL FULFILLMENT OF THE REQUIREMENTS  
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1989

#### ACKNOWLEDGMENTS

I wish to thank all those with whom I enjoyed discussing ecology during my student years. In particular, I want to thank my major advisor, Jack Putz, for the enthusiasm with which he supported my work, and for all his encouragement, guidance, and friendship. I would also like to thank my other committee members, Walter Judd, Kenneth Buhr, and Hugh Popenoe for reviewing the dissertation, and supplying me with suggestions and ideas. Thanks to Peter Feinsinger for encouragement, ideas, and ecological enjoyment, and to Kenneth Portier for statistical advice. I would like to thank Jack Ewel for his advice and time spent with me. I wish to collectively acknowledge my office-mates (past and present members of the 414 Carr Hall crew), and native and international friends who made me feel happy, and who supported me professionally and emotionally during all these years.

Many people helped me in Panama, but I particularly would like to thank Gordon McPherson for taking me for the first time to the El Llano-Carti road and helping me to identify plant species; Alan Smith for encouragement, advice and computerized analysis of hemispherical canopy photographs; and Nancy Garwood for teaching me how to identify seedlings. To Don Windsor, Argelis Roman, friends on Barro Colorado Island, and the Smithsonian Tropical Research Institute staff in general, thanks

for being such a nice people. I am in debt to my field assistants, Hipolito Rodríguez, a local farmer, and Franklin O. Guardia, a biology student, for helping me in all those hot, wet, muddy, wonderful days in the forest. I also thank the Kuna Indians and particularly the PEMASKY people for their great effort in conservation.

I gratefully acknowledge the financial support received from the James Noyes Foundation through the Smithsonian Tropical Research Institute that permitted me to carry out my field work.

## TABLE OF CONTENTS

|                                                        | Page |
|--------------------------------------------------------|------|
| ACKNOWLEDGMENTS. . . . .                               | ii   |
| ABSTRACT . . . . .                                     | vi   |
| <br>CHAPTERS                                           |      |
| I FOREST EDGES AND FRAGMENTED HABITATS . . . . .       | 1    |
| Introduction . . . . .                                 | 1    |
| Forest Edge Characteristics. . . . .                   | 3    |
| Edge Origin. . . . .                                   | 7    |
| Habitat Fragmentation and Disturbance. . . . .         | 9    |
| Objectives . . . . .                                   | 11   |
| II STUDY AREA: FOREST EDGES IN THE EL LLANO-CARTI ROAD | 13   |
| Study Area . . . . .                                   | 13   |
| Kuna Wildlife Project and El Llano-Carti Road. .       | 13   |
| Ecological Conditions. . . . .                         | 15   |
| Study Sites. . . . .                                   | 15   |
| III VEGETATION STRUCTURE AND ENVIRONMENTAL CONDITIONS  |      |
| ON FOREST EDGES. . . . .                               | 21   |
| Introduction . . . . .                                 | 21   |
| Methods. . . . .                                       | 24   |
| Pasture-Forest Environmental Gradients . . . . .       | 24   |
| Forest Vegetation Structure. . . . .                   | 25   |
| Effect of Agricultural Practices on Pasture-Edge       |      |
| Vegetation . . . . .                                   | 25   |
| Effect of Edge Proximity on Dead Tree Density. .       | 27   |
| Data Analysis. . . . .                                 | 28   |
| Results. . . . .                                       | 29   |
| Pasture-Forest Environmental Gradients. . . . .        | 29   |
| Floristic Composition. . . . .                         | 33   |
| Forest Vegetation Structure. . . . .                   | 33   |
| Understory Percent Cover . . . . .                     | 43   |
| Lifeforms. . . . .                                     | 43   |
| Effect of Agricultural Practices on Pasture-Edge       |      |
| Vegetation . . . . .                                   | 43   |
| Effect of Edge Proximity on Dead Tree Density. .       | 47   |
| Discussion . . . . .                                   | 52   |
| IV THE ORIGIN OF EDGE VEGETATION. . . . .              | 59   |
| Introduction . . . . .                                 | 59   |

|                                                  |        |
|--------------------------------------------------|--------|
| Methods. . . . .                                 | 62     |
| Soil Seed Bank along the Future Edge . . . . .   | 62     |
| Seed Germination in Response to Canopy Opening . | 62     |
| Seed Germination in Response to Soil Disturbance | 63     |
| Height Growth of Advance Regeneration . . . . .  | 64     |
| Results. . . . .                                 | 64     |
| Soil Seed Bank along the Future Edge . . . . .   | 64     |
| Seed Germination in Response to Canopy Opening . | 66     |
| Seed Germination in Response to Soil Disturbance | 66     |
| Height Growth of Advance Regeneration . . . . .  | 71     |
| Discussion . . . . .                             | 75     |
| <br>V EPILOGUE . . . . .                         | <br>82 |
| REFERENCES . . . . .                             | 85     |
| APPENDIX A . . . . .                             | 97     |
| APPENDIX B . . . . .                             | 103    |
| APPENDIX C . . . . .                             | 109    |
| BIOGRAPHICAL SKETCH. . . . .                     | 113    |

Abstract of Dissertation Presented to the Graduate School  
of the University of Florida in Partial Fulfillment of the  
Requirements for the Degree of Doctor of Philosophy

DEVELOPMENT OF TROPICAL FOREST EDGE VEGETATION

By

Guadalupe Williams-Linera

May 1989

Chairperson: Dr. Francis E. Putz  
Major Department: Botany

Impacts of forest edges on microenvironmental conditions, vegetation structure, tree mortality, and floristic composition were studied in an experimentally created edge in primary forest and in five forest edges 0.8 to 12 years old in the Tropical Premontane Wet Forest in Panama.

Along transects from clearing to forest interior, the greatest change in temperature and relative humidity occurred between 2.5 and 15 m into the forest. Forest canopy cover increased to and remained at about 94.9-98.7% beyond 5 m into the forest. Density (stems/ha) and basal area ( $m^2/ha$ ) of trees  $< 10$  cm dbh were twice as high on 5- to 12-year-old forest edges as in forest interior. Edge-to-interior ratio of trees that presumably died after edge creation was 14:1. Beyond 15-25 m

into the forest neither environmental conditions nor forest structure were influenced by proximity to the edge.

Relative growth rates of woody plants < 2 m tall over a 10-month period indicated that forest edge plants grew at twice the rate of interior plants. The forest edge also had a higher seedling density and seedling recruitment rate than the forest interior. Seedling survival, however, was lower for edge plants than for forest interior plants. Floristic composition was similar in forest edge and forest interior plots.

A soil seed bank study performed on the experimental edge indicated that seeds of light-demanding woody species were abundant before edge creation. Canopy photographs, germination bioassays, and the large number of germinated seeds in response to soil disturbance treatment confirmed that lateral light penetration into the forest edge was sufficient to promote germination of light-sensitive seeds. Soil disturbance exposed buried seeds to light and increased seedling density, especially of woody secondary species. Light-demanding species were rare in the forest edges in part because soil disturbance did not occur during edge creation. Edge plants were derived primarily from seedlings and saplings present before edge creation.

This study documented the significance of edge vegetation development on buffering forest interiors from conditions in adjacent clearing. Implications for conservation are clear. It is advisable to not disturb soil and vegetation on the edge of forest reserves to surround forests by a buffer zone of primary vegetation.

## CHAPTER I FOREST EDGES AND FRAGMENTED HABITATS

### Introduction

The perception of community edges depends to some extent on the underlying community concept. The debate concerning the nature of communities focuses on whether plant species are assembled into discrete units or whether every species distribution is independent of its associates. The Clementsian interpretation, also called the community-unit concept (Whittaker 1975), assumes that communities are natural, discrete, recognizable groups of species with interdependent functional relationships (Clements 1936). In this case, the community limit is an "ecotone" or transition zone where one vegetation type contacts another. In contrast to the community-unit theory, the individualistic concept states that the spatial distribution of every plant species depends upon its individual peculiarities of migration and environmental requirements (Gleason 1926). If environmental changes are gradual, the apparent distinctness of communities is lost and identifiable limits do not exist; exceptions exist where there are sudden discontinuities in the environment, such as changes in soil parent material, changes in elevation or slope aspect, advance of fire, or presence of landslide rubble (Gleason 1926, Barbour et al. 1980). The individualistic concept is linked to a continuum view of

populations along gradients (Curtis and McIntosh 1951, Whittaker 1975).

Recently, biotic boundaries along environmental gradients have been located using statistical techniques such as probabilistic similarity techniques on species presence/absence information among locations (McCoy et al. 1986), or analyses of deviance on predicted and observed pattern of boundaries along a gradient (Shipley and Keddy 1987). Species distribution boundaries that are clustered along gradients contradict the individualistic hypothesis, but boundaries that are not consistently clustered contradict the community-unit hypothesis (Shipley and Keddy 1987).

Another viewpoint presented in systems ecology reduces edges to nothing more than boxed lines indicating the boundaries of the portion of the world in which one is interested (Odum 1983). Different community-boundary perceptions are complementary and useful in different ecological circumstances. Whittaker (1975) considers that "there is no real conflict between the principle that communities are generally continuous with one another, and the practice of classifying these communities as a means of communication about them." Also, ecotones can be regarded as part of an environmental gradient connecting different communities, and edges can be considered as "microecoclines" (Whittaker, personal communication, cited in Wales 1972).

When communities have been described, the borders are usually not defined because marked transition zones are not really needed to characterize a community. It is generally

enough to assume that if ecosystem composition is different in two areas, some change must occur between them--perhaps gradually, perhaps more steeply (Margalef 1978). Natural and human-made edges are significant in preservation of whole ecosystems and remnant forest or forest islands, in insect pest management and natural regeneration during silvicultural practices, and in their affect on wildlife abundance and interspecific interactions (Levenson 1981, Ranney et al. 1981, Noss 1983, Lovejoy et al. 1983, 1984, 1986, Leopold 1933, Johnston 1947, Gates and Gysel 1978, Harris and McElveen 1981, Noss 1983, Wilcove et al. 1986, Andrén and Angelstam 1988, Small and Hunter 1988, Stanton 1983, Risser et al. 1984, Tryon and Trimble 1969). Although edge importance is recognized, edges have been insufficiently studied.

#### Forest Edge Characteristics

Several authors have tried to characterize, delimit, describe, and understand edge dynamics. Forest edges have been conceptualized as distinct habitats (Johnston 1947, Gates and Gysel 1978), semipermeable membranes or skins between areas with different resource concentrations (Jenny 1961, Wiens et al. 1985, Oldeman 1986), and buffer zones against disturbance propagation (Risser et al. 1984, Wiens et al. 1985). They have been compared to forest light gaps (Wales 1972, Levenson 1981). Even idealized edge components have been defined and described:

...A herbaceous layer like the hem of a skirt, called a saum or perennial herb border, is on the outside. Then comes a woody layer of shrubs and small trees called a mantel or woody mantle (named for an overcoat that surrounds and

protects the forest interior from outside weather) that in turn borders or is under the canopy trees. The juxtaposition of the outer edges of saum, mantel, and canopy varies according to how close a disturbance, such as plowing in the open area, comes to the trunks and canopy trees. If disturbance is close to the tree trunk and canopy branches overlap the field, usually the mantel is poorly developed and the saum is sparse. However, if the disturbance line lies outside the tree canopy branches, a well-developed saum is usually present with a dense and wide mantel extending back to the tree trunk area (Forman and Godron 1986:108-109).

Forest edges are distinct habitats in the sense that vegetation structure and biota differ from either contiguous community (Leopold 1933, Ranney et al. 1981). Where edges from different vegetational types meet, wildlife is often more abundant because food and cover needed by different animals converge (Leopold 1933). Although some birds that inhabit forest edges display specific behavior patterns appropriate only for edges (Johnston 1947), the variety and abundance of birds, and concentration of nests, increase density-dependent mortality, turning forest edges into "ecological traps" (Gates and Gysel 1978) because of increased nest predation (Wilcove et al. 1986, Andr  n and Angelstam 1988).

Edges may insulate a forest but they do not make it ecologically independent of adjacent clearings. Many fluxes occur through edges. Fluxes of energy, nutrients, and organisms are important in both directions (Forman 1981, Forman and Godron 1981, Risser et al. 1984, White and Pickett 1985). Energy fluxes in form of heat, wind, or light penetrate into forest edges (Ranney 1977). Nutrient fluxes cross boundaries between agricultural fields and riparian forests affecting water quality (Lowrance et al. 1984). Also, many types of animals forage from

one side to another (Forman and Godron 1981), or transport macrodetritus, whole organisms and seeds (Wiens et al. 1985).

Disturbance enters forest interiors through edges, but at the same time edges are potential barriers to the spread of disturbance from a field into a forest. For instance, fires set to control weeds in degraded pastures in eastern Amazonia commonly spread into adjacent forests. Fire readily spreads through exploited (selectively logged) forests, causing extensive damage, but fires reaching the edge of unexploited forests quickly die out. It is critical to recognize that whereas exploited forest edges in the Amazon burn readily, fires generally do not penetrate more than a few meters into virgin, unlogged forest (Uhl and Buschbacher 1985).

After the forest edge vegetation develops, the forest interior is less affected by disturbances coming from the adjacent clearing such as fire, wind, or higher temperature. To minimize edge effects on the forest interior by increasing the rate of buffer vegetation development, it has been proposed to plant fast-growing species that produce dense foliage on forest edges (Ranney et al. 1981, Lovejoy et al. 1984).

Forest edge studies are in their inception. Therefore, light gaps are frequently used as a reference point when edge vegetation structure, function, or floristic composition is described. For instance, Wales (1972) suggested that edges share with forest gaps both a vertical and horizontal structure intermediate to that of well-developed forest and adjacent old

fields. Levenson (1981) mentioned that gaps within the forest function in much the same manner as the edge. The frequency of gaps can contribute greatly to making a large woodlot no more than a highly convoluted edge. Similarly, cutting the edge vegetation or dividing a large woodlot may destroy the mesophytic environment of the system.

Edges and light gaps are both non-homogeneous habitats with different plant species suited along their complex microenvironmental gradients (Bazzaz 1984, Brokaw 1987, Hubbell and Foster 1988). Presumably, more species can effectively subdivide a long gradient (large environmental differences) than a short one; yet data from experimental studies, to determine whether these environmental gradients are subdivided, are lacking (Denslow 1985). There is, however, evidence that light-demanding species in tropical forest canopy gaps are differentially distributed among gaps of different sizes, and perhaps the gap-size tolerance limits observed are actually the manifestation of niche partitioning along a gap center-to-edge axis (Brokaw 1987). Given the complexity of environmental gradients, the generalization of "edge environment" as well as "gap environment" has limited utility.

With respect to floristic composition, several authors have reported that shade-intolerant species are prevalent within both forest edges and forest gaps (Wales 1972, Thompson and Willson 1978, Ranney et al. 1981). Another author suggested that although many species seem to be primarily edge species with only occasional occurrences within more extensive communities, some

are known to occur commonly in the extensive vegetation type of one zone while remaining edge species in another (Grubb 1985). In any case, Grubb (1985) considers that the whole issue of edge plants, and the characteristics that separate them from plants of gaps in the nearby extensive vegetation types, are worthy of much closer attention from ecologists.

### Edge Origin

Natural landscapes are typically characterized by spatial discontinuities in physical and biological conditions (Forman and Godron 1981, Wiens et al. 1985). The resulting vegetational units are connected through their boundaries or transition zones. They can be broad and undefined, occurring along gradually changing ecological conditions, or sharp and easy to distinguish, where physical boundaries create abrupt changes in vegetation (Ricklefs 1979, Forman and Godron 1981).

One of the most studied transition zones is the temperate zone forest-prairie ecotone. This ecotone resulted from a combination of fire disturbance and established vegetation, a geographic pattern of physical firebreaks, and larger climatic cycles that were favorable to the invasion of prairie by forest or marginal brushland (Buell and Cantlon 1951, Grimm 1984). Sharp edges can be found between heath balds and forest in the Southern Appalachians; the presence of heath balds is correlated with steep slopes and leached acid soils. Their origin is unclear but is probably climatic (Brown 1941, Whittaker 1963, Braun 1974).

Biotic factors such as animal foraging activities or allelopathy can also create edges. For instance, between shrub (chaparral and sage scrub) and grass communities in coastal California there is often a zone bare of vegetation. It has been hypothesized that this zone is maintained by increased animal activity, because it is a safe border for small mammals and birds that feed in the grassland and take cover in the adjacent chaparral (Bartholomew 1970). An alternative is that the zone results from allelochemical interactions (Wells 1964, Muller and Muller 1964).

Other types of natural edges originate by natural physical disturbances such as fires, storms, landslides, or winds. Biological disturbances, such as predation or grazing, also create patches and consequently edges (White 1979, Sprugel and Bormann 1981, Sousa 1984, Wiens et al. 1985).

Human-induced disturbance of natural landscapes has affected enormous areas, fragmenting whole habitats. Deforestation and forest fragmentation have increased natural landscape heterogeneity, creating a human-made spatial pattern in which patches of different vegetational types and ages are juxtaposed. As a consequence, the extent of edge is increasing worldwide (Burgess and Sharpe 1981, Foster 1980, Soulé 1986, Verner et al. 1986).

In temperate forest regions most edges are artifacts of human-modified landscapes. They are permanent, yet dynamic and highly associated with the impacts of urbanization (Ranney et al. 1981). In tropical forest zones, in contrast, edges are

associated more with impacts of rural development than with urbanization. Also, forest edges, in general, are less permanent because agricultural frontiers are advancing yearly into the forest (see Parsons 1976, Myers 1981, Faber et al. 1986).

### Habitat Fragmentation and Disturbance

Disturbance per se and concomitant habitat fragmentation or patchiness have long been observed and described, but the appearance of these as part of the theory of community and ecosystem dynamics is only a recent development in ecology (e.g., Whittaker and Levin 1977, Mooney and Godron 1983a, Pickett and White 1985a; but see Watt 1947). In fact, many studies indicate that traditional community approaches have underestimated the role of disturbance in ecosystem dynamics. This role is as important as biological interactions such as competition and predation, which have received more empirical and theoretical attention from ecologists (Levin and Paine 1974, Sprugel 1976, Sousa 1984, Pickett and White 1985b).

Disturbance implies partial or total destruction of plant biomass (Grime 1979) and changes in resources, substrate availability, and physical environment (White and Pickett 1985). Prominent forest edges are created by large-scale disturbances, which are often human-generated. Some human disturbances of ecosystems closely mimic natural disturbances, but, more generally, human-induced disturbances contrast with natural disturbances in kind, intensity, and frequency (Reiners 1983, Mooney and Godron 1983b). Agricultural practices, for example,

range from increasing the frequency of gap formation in tropical forest by shifting agriculture to annual disturbance by tillage agriculture (Reiners 1983).

Beyond physically disturbed sites, indirect effects may modify environmental conditions of contiguous areas. For instance, deforestation not only results in clearings but also influences the remaining forest. There is a persistent relationship between the predominant mode by which disturbed sites are recolonized and patch size. At one extreme are large clearings with no survivors which undergo a secondary successional process. At the other extreme, the smallest disturbances are filled almost exclusively, and relatively quickly, by the vegetative growth of survivors living either within the clearing or on its edge. Little or no successional replacement takes place in this case (Sousa 1984). Miller (1982) constructed a model incorporating disturbance size and frequency, and community diversity, and concluded that large disturbances may favor colonizing light-demanding species and small disturbances may favor competitive primary species.

*Disturbance*

Disturbance is an integral part of ecosystems. It creates a mosaic landscape in which patch edges limit and connect environmental discontinuities and different vegetational types. Edges are ecosystem limits. Edge structure depends on vegetation age, topography, location, disturbance regime, and conservation practices. Edges are entities that deserve to be studied in more detail.

This investigation was designed to decipher patterns and processes of tropical forest edge vegetation. A description of the geographical area in which this research was conducted is presented in Chapter II. Chapter III includes the descriptive part of the research and focuses on vegetational structure, environmental gradients, floristic composition, and tree mortality of different aged edges. In Chapter IV the experimental portion of the research is presented; the studies described were designed to elucidate the dynamics of edge vegetation development. Chapter V consists of an attempt to incorporate the new information gathered in this study into a general, integrated perspective on edges.

#### Objectives

The objectives of the descriptive part of the investigation were the following:

1. Examine the impact of edge creation on environmental conditions and vegetation structure of pastures and adjacent primary forest.
2. Investigate how vegetation structure, tree mortality, and environmental gradients are interrelated on forest edges.
3. Depict the importance of cattle grazing and agricultural practices to maintenance of the forest edge structure and floristic composition.

The objectives of the experimental part of the investigation were the following:

1. Determine why light-demanding tree species are rare at the surveyed forest edges.

2. Find out whether edge plants come from the soil seed bank, or from seedlings and saplings present before the edge was created.

3. Determine the importance of canopy and soil disturbances in the establishment of edge vegetation.

CHAPTER II  
STUDY AREA: FOREST EDGES IN THE EL LLANO-CARTI ROAD

Study Area

The study area is located near the border between the San Blas Comarca (Kuna Yala, literally Kuna earth) and Panama Province, Republic of Panama, between km 10 and km 17 along the El Llano-Carti road ( $9^{\circ}15' N$  and  $9^{\circ}18' N$ ,  $78^{\circ}55' W$  and  $78^{\circ}58' W$ ). The elevation ranged from 220 to 325 m (Figure 1). This area was chosen because primary forest occurs adjacent to areas that have been converted from forest to pasture.

Kuna Wildlife Project and El Llano-Carti Road

Kuna Yala is less than 200 km from Panama City, but its forests are primeval and wildlife abundant, partially because the El Llano-Carti road was only opened in the early 1970s. It was the first all-weather access road into the Kuna Yala on the northeast coast of Panama. The construction of the road facilitated access and thereby increased opportunity for colonization by landless peasants from other provinces. On the basis of a treaty signed in 1925 with the Panamanian Government, the Kuna Indians are the only people permitted to own land in the 3106 km<sup>2</sup> San Blas Comarca and to make political decisions relevant to their land (Arias and Houseal 1986, Huber 1986). To prevent squatters from settling in Kuna Yala, the Kunas decided to establish a Kuna presence, without destroying the forest, by

setting up a major reserve. The idea of scientific tourism emerged to attract photographers, bird watchers, university students, and scientists to study the undisturbed rainforest. In 1976 the Kuna Wildlands Project (PEMASKY) started. In 1987 the first accommodations were completed and visitors started arriving.

The Pacific slope of the cordillera just outside the reserve boundaries has been deforested. The colonizers were motivated by the "unwritten law" that "land that they improve will be theirs." Land improvement was interpreted as cutting the forest. Thus, deforestation was integrated into one of the national development plans popularly called "The Conquest of the Atlantic Region." When the road was opened, newcomers and peasants already established, able to prove land use, received land property titles. Several hectares of undisturbed forest were cut down to demonstrate land improvements, rice or corn was planted, and later the land was converted to pastures. Unfortunately, when the forests are felled, the peasants do not find themselves in a good economic position. The fragile soil and steep slopes are incapable of supporting permanent crops and cattle ranching. The devastation stands in sharp contrast with Kuna Yala. Deforestation has stopped at the reserve edges on the non-Kuna side because colonizers are using the continental divide as the back limit of their properties and because of the Kuna presence in Nusagandi, the headquarters of PEMASKY (Breslin and Chapin 1984, Huber 1986, PEMASKY 1985, Arias and Houseal 1986).

### Ecological Conditions

The study area is in the Tropical Premontane Wet Forest life zone (Tosi 1971). Temperature and precipitation records exist for the nearby field headquarters of the PEMASKY project at Nusagandi (Figure 1) since August 1984. The average temperature is 26°C and varies more on a diurnal than on an annual basis. Mean annual minimum and maximum temperatures (1984-1986) were 21 °C and 29 °C, respectively. Annual average relative humidity is 86%. Mean annual rainfall is about 3500 mm; the drier season (< 100 mm/mo) extends from January through March (Figure 2).

### Study Sites

Five pastures adjacent to primary forest on the Pacific side of the continental divide were selected for study. Pasture age was determined through interviews with local inhabitants. The disturbance history was similar in all the sites. The process of creating pastures begins with cutting several hectares of forest during the dry season and burning the area after the vegetation dries, in general within a month. With the first rains (April and May), typically rice or corn is planted for one or two years, depending on soil fertility. During the last crop, seeds of the exotic grass "ratana" (Ischaemum indicum (Houtt.) Merrill) are broadcast, and after the last crop the pasture is ready for cattle. Wire fences between forest and pasture were only present in the 7-year-old site. Cattle penetrate the forest edge where hunter trails start or where wood has been extracted. The study sites showed no indication that cattle had penetrated into the

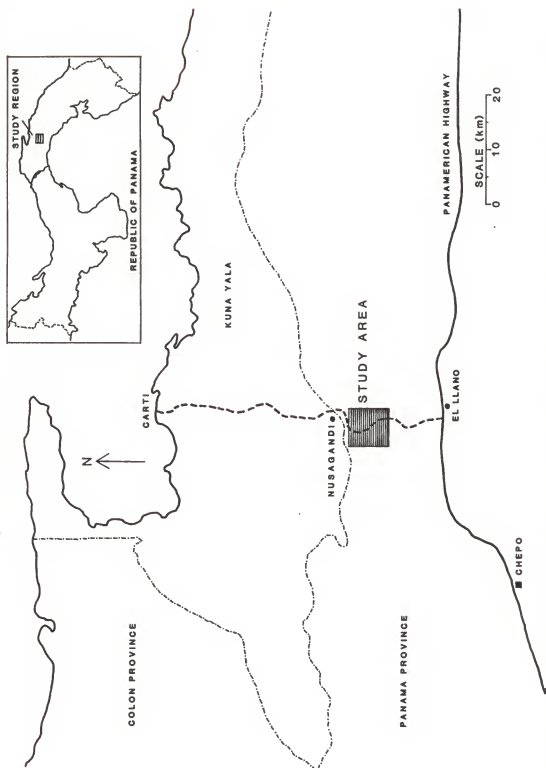


Figure 1. Location of the study area near the border between Panama Province and Kuna Yala in the Republic of Panama.

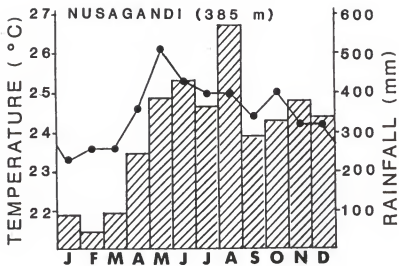


Figure 2. Climate diagram (August 1984 to December 1986) of Nusagandi station, located 3 to 11 km from the study sites. Dots represent mean monthly temperature ( $^{\circ}\text{C}$ ) and bars represent monthly rainfall (mm).

forest edge or forest interior. Also, no evidence of fire into the forest edges was detected in any study site. Due to weeding practices and cattle grazing, very few reproducing pioneer trees were present in the pastures.

The topography of each study site was mapped with a Suunto inclinometer. Slopes were measured in 50 x 60 m plots every 10 m in parallel and perpendicular planes to the forest edge (Appendix A). Although topography has been reported to be linked to tree density and treefall (Grubb et al. 1963, Heinsdijk 1957, cited in UNESCO 1978, Brokaw 1985a), in all study sites there was no correlation between degree of slope and density of trees > 5 cm dbh or treefall frequency.

At each study site five composite soil samples from the forest (10-20 m from the border) were taken from the 0-10 cm and 10-30 cm depth intervals with an auger. At sites where the edges were 5 and 12 years old, two transects were sampled. Soil was collected in the pasture (10-20 m from the border), at the pasture-forest border, and in the forest.

The soils at all sites are very acid and clayey with high contents of exchangeable Al, and organic matter, and low contents of P, K, Ca, and Mg. Significant differences were not detected among sites or transects within sites, but this is not surprising considering the small number of samples analyzed (soil procedures and results are outlined in Appendix B).

Ten-month-old site. This site is located at km 17 on the east side of the El Llano-Carti road. The elevation is 330 m and slopes range from 10 to 30%; the forest faces NW (Appendix A-1).

An area of 5 ha of forest was cut in February 1986, and after burning it was planted with rice. Rice was still being grown when the study was carried out.

Five-year-old site. This site is located at km 9.5 on the west side of the El Llano-Carti road. The elevation is 315 m and slopes range from 20 to 60%; the forest faces NE (Appendix A-2). The forest was cleared during the 1981 dry season, and rice and corn were planted for two years before this site was converted to a pasture. The 30 ha pasture supported 20 head of cattle and one horse at the beginning of the study period but after six months the stock was reduced to 5 cattle because of the degraded condition of the pasture.

Seven-year-old site. This site is located at km 17 on the west side of the El Llano-Carti road. The elevation is 325 m and slopes range from 10 to 30%; the forest faces N (Appendix A-3). The clearing was carried out during the 1979 dry season, and the site was planted with rice for a year before it was converted to pasture. The pasture has an area of approximately 10 ha. During the study period, it supported 8 head of cattle and 2 horses. This study site was the only one with wire fences between pasture and forest.

Ten-year-old site. This site is located near a lateral road that diverges at km 14 on the east side of the El Llano-Carti road. The elevation is 340 m and the slope is 20 to 60%, and the forest faces SW. The clearing was made in 1976 (Appendix A-4). The pasture is contiguous to the 12-year-old site pasture.

Together they have an area of approximately 30 ha. They support 20 head of cattle and 4 horses most of the year.

Twelve-year-old site. This site is adjacent to the ten-year-old site; they are located along the same ridge but initially were separated by a deep forested gorge. Elevation and slope are the same as the 10-year-old site; the forest faces NW. The clearing was made in 1974 (Appendix A-5).

Newly created edge. The experimental edge was created in March 1987, when a local farmer cut 1 ha of primary forest as part of shifting agriculture activities. Before the clearcut the farmer showed me the area that he was planning to cut. We marked the future edge with flagging tape and permanent plots with rods. The future edge was parallel to the hill slope on a small crest. During the clearcut, the farmer directed the felling of trees away from the forest and marked plots were not damaged. The study site was surrounded by undisturbed primary forest and 3 km from the nearest pasture; the elevation is 220 m and slopes are around 40%.

The descriptive part of this investigation, presented in Chapter III, was carried out in the 10-month, 5-, 7-, 10-, and 12-year-old sites. The experimental part, presented in Chapter IV, was performed along the newly created edge.

CHAPTER III  
VEGETATION STRUCTURE AND ENVIRONMENTAL CONDITIONS ON  
FOREST EDGES

Introduction

When forests are cut and sharp edges are created the environmental conditions at the edge of the remaining forest change markedly (Lee 1978, Lal 1987). Canopy removal increases the amount of solar radiation and rainfall that reach the soil surface. Wind velocity is also affected by the forest opening, being reduced within the forest. The high relative humidity commonly observed in a forest interior decreases in clearings because of increased air temperature, increased wind velocity, and decreased transpiration (Schulz 1960, Grubb and Whitmore 1966, Raynor 1969, Lawson et al. 1970, Lee 1978, Lawson et al. 1981, Fritschen 1985, Lal 1987). Environmental conditions on forest edges undoubtedly are intermediate to those prevalent in clearings and forest interiors. There is, however, virtually no information concerning the depth into the tropical forest at which the influence of the clearing on environmental conditions becomes negligible.

Vegetation structure and floristic composition along edges and some distance inside the forest reflect changes in abiotic conditions (Wales 1972, Ranney et al. 1981, Lovejoy et al. 1983, Miller and Lin 1985). For instance, a structural analysis of temperate deciduous forest edges demonstrated that basal area and

stem density of trees and saplings decrease from the edge toward the interior for a distance of about 15 m (Ranney et al. 1981). In an Acer rubrum (red maple) forest edge, leaf density is twice as large on the forest edge than in the interior (Miller and Lin 1985). Temperate forest edge trees often develop low and thick branches on the field sides, and asymmetrical boles that lean toward the clearing (Wales 1972, Ranney 1977, Levenson 1981). Tropical forest edges have been described as marginal communities, unlike the forest interior: dense strips with many small trees, vines, woody climbers and, heliophilous ground herbs (Longman and Jenik 1974). Within 5 years of isolation, forest reserves in Central Amazonia reportedly develop a 10-25 m wide wind-break edge of vines and secondary vegetation that shades the forest interior, making it noticeably darker and more humid than it was immediately after isolation (Lovejoy et al. 1986). Although the abundance of tropical forest edges increases with deforestation, and edges are potentially important for forest preservation, data on vegetation structure of tropical forest edges are for the most part lacking.

It has been suggested that species compositions for forest edge and interior are different. Temperate forest edges are reported to have more shade-intolerant individuals than forest interiors (Wales 1972, Ranney et al. 1981). In Central Amazonia, secondary species are observed to invade forest reserve edges and create a band of secondary vegetation among the trunks of dead and fallen trees abundant on edges (Lovejoy et al. 1984).

Proximity to the remaining forest may affect vegetation structure and plant species composition in clearings. For instance, initial invasion of shrubs into prairie edge has been suggested as a prerequisite for a successful invasion of hardwood forest species (Petranka and McPherson 1979). Plant species that produce fleshy fruits and frugivores that disperse their seeds are concentrated along the edges of temperate forests (Thompson and Willson 1978). Tropical pasture-edge trees produce more fruits than forest interior trees of Stemmademia donnell-smithii (Rose) Woodson (Apocynaceae), a species with bird-dispersed fruit (McDiarmid et al. 1977). In this way, pastures adjacent to forest are probably receiving more propagules than pastures farther from forest; edge maintenance is consequently possible only by continued agricultural activities in the pasture.

When isolated from the protection of neighboring vegetation, forest-grown trees have higher probabilities of dying than forest-interior trees because of their exposure to gusty wind and to other different environmental conditions (Brokaw 1985b, Hubbell and Foster 1988, Lawton and Putz 1988). In northeastern United States evergreen forest (Abies balsamea forest), areas closer to clearcut edges are subjected to more uprooting than areas farther from edges (Gordon 1973). In general, increased tree death occurs primarily among edge trees (Sprugel and Bormann 1981). Also, in Central Amazonia an increase in the number of wind-thrown and broken trees has been observed following creation of edges (Lovejoy et al. 1986).

### Methods

In this part of the investigation the impact of edge creation on vegetation structure, tree mortality, and environmental gradients on tropical forest edges are examined. The study was carried out in the five primary forest edges contiguous to the pastures described in Chapter II.

#### Pasture-Forest Environmental Gradients

Maximum and minimum temperatures and relative humidity were measured along transects at each of the study sites. Each transect was 70 m long, extending from 25 m into the pasture to 45 m into the forest. Sun shelters for the thermometers were constructed at 150 cm above the ground, using palm fronds. Eight weather shelters were placed at 10 m intervals along each transect, and one more was placed on each pasture-forest border. Temperature and relative humidity (measured using a sling psychrometer) were recorded three times a week for two weeks at each site during the dry season (January-March 1987). Measurements were made one site at a time; this explains some of the differences in absolute values of temperature and relative humidity among sites.

Overstory density was estimated by hemispherical canopy photographs (taken with a fish-eye lens placed 60 cm above the ground). The photographs were taken at 0, 5, 15, and 25 m along two transects extending from the pasture-forest border into the forest at each study site. The negatives were analyzed for percent canopy openness using a computerized canopy photograph analysis program (Becker et al. unpub.).

### Forest Vegetation Structure

At each study site, vegetation was characterized along four randomly located 10-m-wide strips from the pasture-forest border to 20 m into the forest. The belt transects were divided into 5 x 10 m plots parallel to the edge. The number and dbh (diameter at 1.3 m) of all trees and lianas > 5 cm dbh were recorded. In a 5 x 5 m subplot randomly selected in each of the 10 x 5 m plots, the number and dbh of all woody plants > 2 m tall but < 5 cm dbh were recorded. Smaller woody and herbaceous plants were recorded by life form as percent cover in a randomly located 2 x 2 m subplot in each 10 x 5 m plots (Figure 3). Forest vegetation height adjacent to pastures was measured with a Haga inclinometer.

To assess how far the effect of proximity to the edge penetrates into forest vegetation, the transects were extended to 60 m into the forest. Plots similar to those described above for plants < 5 cm dbh were continued at intervals of 20 m along two transects. Point-quarter samples of trees (Cottam and Curtis 1956) were taken at 20 m intervals along each 60 m transect (Figure 3). Along each transect the dbh and distance to trees 5-9.9, 10-19.9, and > 20 cm dbh were recorded. Voucher specimens from trees were deposited at the University of Panama Herbarium.

### Effect of Agricultural Practices on Pasture-Edge Vegetation

Permanent plots were established to assess the role of cattle grazing and pasture maintenance on near-edge vegetation. Adjacent to 5-, 7-, 10-, and 12-year-old edges, two series of 2 x 2 m plots were set up from the edge to 20 m into the pasture

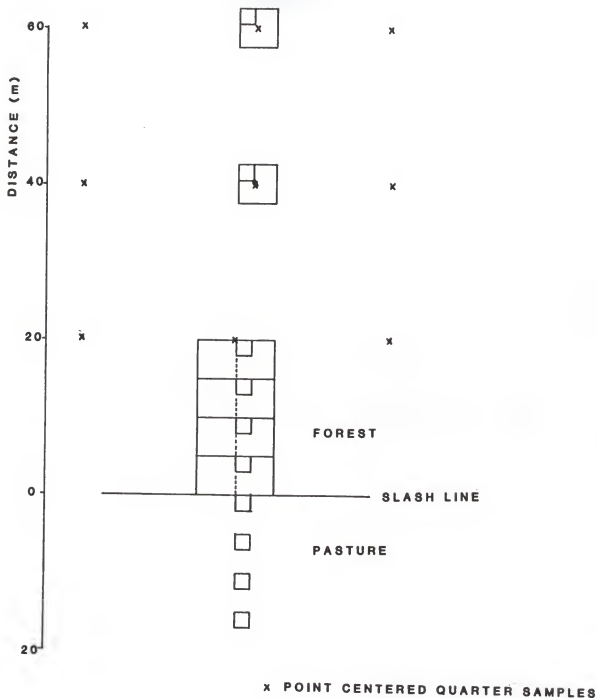


Figure 3. Sampling unit. Woody plants  $> 5$  cm dbh were recorded in the  $10 \times 5$  m plots and in point centered quarter samples. Woody plants  $< 5$  cm dbh and  $> 2$  m tall were recorded in the  $5 \times 5$  m plots. Smaller woody and herbaceous forest and pasture plants were recorded in the  $2 \times 2$  m plots.

(Figure 3). To exclude cattle and pasture maintenance, a barbed-wire fence was built around one series of plots at each site, and the other was used as a control. The fence was located 1 m outside of the plots. Percent cover, average plant height by life form, and floristic composition were recorded before construction of the exclosures (August-September 1986) and again in February, June, and November 1987.

#### Effect of Edge Proximity on Dead Tree Density

To assess the effect of edge proximity on tree mortality, all fallen, broken, or standing dead trees in a 50 x 60 m plot at each of the five study sites were counted. The short axis of the plot was the forest-pasture boundary. Each plot was divided into strips 50 m long by 5 m wide. Tree death was assessed as a function of distance from the edge. In each strip, the number of dead trees and the apparent mode of death (broken, uprooted, or died standing), diameter class (5-9.9, 10-19.9, 20-29.9, and > 30 cm dbh), and decay state of each were recorded.

The impact of edges on tree death cannot, however, be assessed using all dead trees, because some undoubtedly died prior to edge creation. Therefore, decay classes were used to estimate when the trees had died. The decay classes used in this study (adapted from Maser and Trappe 1984) were the following:

- Class 1. Mostly intact and undecayed trees, small twigs and even leaves present.
- Class 2. Bark intact, branches present.
- Class 3. Pieces of bark start to slough off but wood is still hard.

Class 4. Bark generally absent, wood starts to rot.

Class 5. Bole easily breaks down into small pieces of rotten wood when it is struck.

Classes 1 and 2 were assumed to include trees that died after edge creation; classes 4 and 5 include trees that presumably died prior to edge creation in all age edges. Class 3 was used as an intermediate class for trees that had likely died before edge creation in the youngest edges but probably died after edge creation in the oldest edges.

### Data Analysis

To estimate distances at which the edge effect can be detected in both pasture and forest, environmental data were fitted to a post hoc nonlinear regression model. Maximum temperature was selected because relative humidity is correlated with temperature.

$$\begin{aligned}
 y &= a_0; & (D < y_0) \\
 &= b_0 + b_1 D; & (y_0 < D < y_1) \\
 &= c_0; & (D > y_1) \\
 &\text{at } y = y_0, a_0 = b_0 + b_1 D_0, \\
 &\text{at } y = y_1, c_0 = b_0 + b_1 D_1,
 \end{aligned}$$

where  $D$  is distance along the pasture-forest gradient,  $y_0$  is estimated distance into pasture,  $y_1$  is estimated distance into the forest,  $a_0$  is predicted temperature at  $y_0$ , and  $c_0$  is predicted temperature at  $y_1$ .

Study sites of the same age were difficult to find in the area. ANOVAs were performed using randomly located transects as replicates (I recognize that these are actually pseudoreplicates

sensu Hurlbert (1984), but there was no alternative). All proportions were arcsine square root transformed before being subjected to parametric tests. ANOVA and t-test were performed with Systat (Wilkinson 1986) and nonlinear fitting with SAS (SAS 1984). Means were compared using the Waller-Duncan Bayes LSD; its advantage, in contrast to experimentwise error rate approaches, is that its power does not decrease as the number of means increases (Petersen 1985). Variation about the mean is reported as mean  $\pm$  one standard error, unless specified otherwise.

## Results

### Pasture-Forest Environmental Gradients

In the pastures 25 m from the forest border the average maximum and minimum temperatures during the 1987 dry season were 1.5 to 3.1 °C and 0 to 1.0 °C higher, respectively, than 15-45 m into the forest. Midday relative humidity was 7% lower on the average in the clearing than 15-45 m into the forest (Figure 4). Mean maximum and minimum temperatures and relative humidities along transects are presented in Appendix C.

Maximum temperature and relative humidity changed gradually along pasture-to-forest interior transects in all sites (Figure 4). Since relative humidity is related to temperature, maximum temperature data were used in a nonlinear model to estimate the distance at which environmental conditions were affected by the presence of the edge. The greatest change in maximum temperature (and consequently in relative humidity) occurred between 0.7 to 10.5 m into the pasture and 2.5 to 15 m into the forest

Figure 4. Maximum and minimum temperatures and percent of relative humidity along transects from 25 m into the pasture to 45 m into the forest in the 0.8-, 5-, 7-, 10-, and 12-year-old study sites.

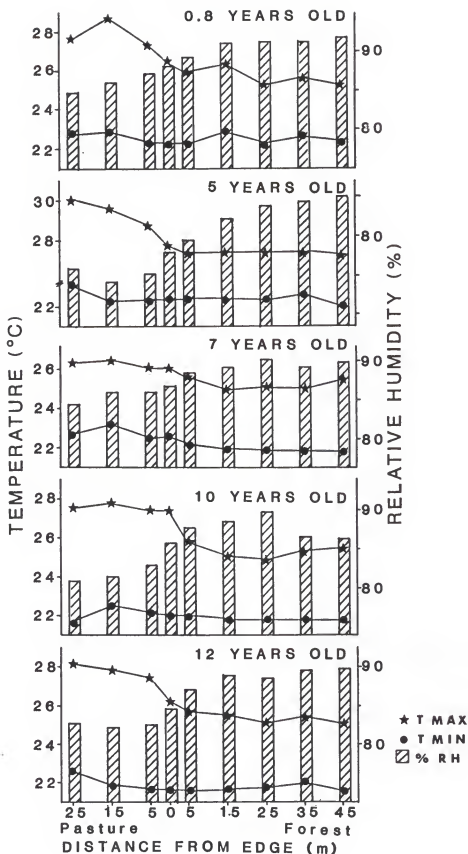


Table 1. Estimated distance (m) of edge effect on microenvironmental conditions into the clearing (y0) and into the forest (y1), lower and upper confidence intervals, and predicted maximum temperature at y0 (a0) and at y1 (c0). The clearing-pasture border is 0 m.

| Edge<br>(yr) | Clearing  |                            |      |            | Forest    |                            |      |            |
|--------------|-----------|----------------------------|------|------------|-----------|----------------------------|------|------------|
|              | y0<br>(m) | 95% Confidence<br>Interval |      | a0<br>(oC) | y1<br>(m) | 95% Confidence<br>Interval |      | c0<br>(oC) |
| 0.8          | -9.4      | -15.5                      | -3.3 | 27.9       | 6.9       | 1.5                        | 12.4 | 25.7       |
| 5            | -11.0     | -23.2                      | 1.3  | 29.9       | 2.5       | -5.0                       | 10.0 | 27.4       |
| 7            | -10.5     | -18.2                      | -2.8 | 26.4       | 15.0      | 7.1                        | 22.9 | 25.2       |
| 10           | -0.7      | -1.1                       | -0.2 | 27.6       | 6.5       | 4.8                        | 8.3  | 25.2       |
| 12           | -9.0      | -12.5                      | -5.6 | 28.1       | 6.7       | 3.4                        | 10.0 | 25.4       |

(Table 1). These distances, however, did not consistently decrease with increase in age edge. Beyond 15 m into the forest, changes in maximum temperature were non-significant.

Along the transects into the forest the canopy was most open at the clearing-forest borders (Figure 5). The 0.8-year-old site also had a higher percent of canopy openness at 5 m from the border than at 15 and 25 m into the forest (one-way ANOVA,  $F=67.06$ ,  $F=136.06$ ,  $F=59.03$ ,  $F=19.67$ ,  $F=33.37$ , for 0.8-, 5-, 7-, 10-, 12-year-old sites, respectively,  $df=3$ ,  $P < .01$ ; Waller-Duncan Bayes LSD,  $P < .05$ ).

#### Floristic Composition

A total of 56 families were represented by woody plants > 2 m tall (Table 2). Plant species composition was similar in forest interiors and forest edges; light-demanding species such as Cecropia spp. (14 individuals out of 2738), Vismia macrophylla (4 individuals), or Palicourea sp. (38 individuals) were not more abundant along forest edges than in forest interior.

#### Forest Vegetation Structure

Density (stems/ha) and basal area ( $m^2/ha$ ) of woody plants < 5 cm dbh decreased with distance from the pasture-forest border into the forest interior (Figure 6), except along the youngest edge. Five-, 10-, and 12-year-old sites showed the highest values for density (one-way ANOVA,  $F=3.12$ ,  $F=2.98$ ,  $F=12.51$ , for 5-, 10-, and 12-year-old sites, respectively,  $df=5$ ,  $P < .05$ ; Waller-Duncan Bayes LSD,  $P < .05$ ) and basal area (one-way ANOVA,  $F=7.02$ ,  $F=4.21$ ,  $F=7.77$ , for 5-, 10-, and 12-year-old sites, respectively,  $df=5$ ,  $P < .01$ ; Waller-Duncan Bayes LSD,  $P < .05$ ).

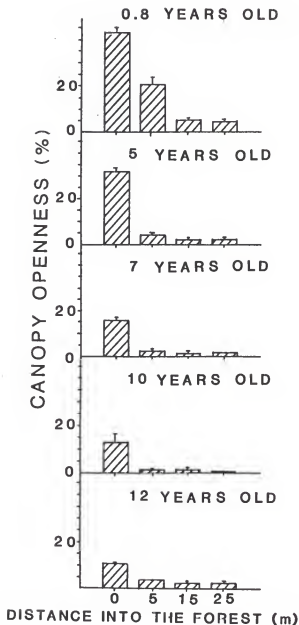


Figure 5. Changes in the percent of canopy openness with distance into the forest in the 0.8-, 5-, 7-, 10-, and 12-year-old study sites.

Table 2. Families and species of woody plants &gt; 2 m tall.

| Family      | Species                      | Individuals<br>No. | Percentage<br>% |
|-------------|------------------------------|--------------------|-----------------|
| Palmae      |                              | 196                | 7.16            |
|             | <u>Socratea durissima</u>    | 54                 |                 |
|             | <u>Iriartea gigantea</u>     | 24                 |                 |
|             | <u>Calyptrogyne</u> spp.     | 21                 |                 |
| Rubiaceae   |                              | 179                | 6.54            |
|             | <u>Palicourea</u> spp.       | 42                 |                 |
|             | <u>Faramea</u> spp.          | 20                 |                 |
|             | <u>Pentagonia</u> spp.       | 16                 |                 |
|             | <u>Cephaelis</u> spp.        | 14                 |                 |
|             | <u>Psychotria</u> spp.       | 11                 |                 |
| Moraceae    |                              | 161                | 5.88            |
|             | <u>Brosimum</u> sp.          | 54                 |                 |
|             | <u>Sorocea</u> spp.          | 13                 |                 |
|             | <u>Cecropia</u> spp.         | 14                 |                 |
|             | <u>Perebea guianensis</u>    | 8                  |                 |
| Guttiferae  |                              | 145                | 5.30            |
|             | <u>Tovomita</u> spp.         | 71                 |                 |
|             | <u>Rheedia</u> spp.          | 18                 |                 |
|             | <u>Symphonia globulifera</u> | 7                  |                 |
| Apocynaceae |                              | 122                | 4.46            |
|             | <u>Bonafousia undulata</u>   | 89                 |                 |
|             | <u>Aspidosperma</u> sp.      | 16                 |                 |
|             | <u>Stemmadenia</u> sp.       | 5                  |                 |
| Leguminosae |                              | 116                | 4.24            |
|             | <u>Inga</u> spp.             | 53                 |                 |
|             | <u>Macrolobium</u> sp.       | 15                 |                 |
|             | <u>Pterocarpus</u> sp.       | 12                 |                 |
|             | <u>Bauhinia</u> spp.         | 7                  |                 |
| Sapotaceae  |                              | 112                | 4.09            |
|             | <u>Manilkara zapota</u>      | 17                 |                 |
|             | <u>Pouteria</u> spp.         | 9                  |                 |

Table 2--continued.

| Family           | Species                          | Individuals<br>No. | Percentage<br>% |
|------------------|----------------------------------|--------------------|-----------------|
| Melastomataceae  |                                  | 93                 | 3.40            |
|                  | <u>Miconia chrysophylla</u>      | 8                  |                 |
|                  | <u>Miconia trinervia</u>         | 4                  |                 |
|                  | <u>Miconia simplex</u>           | 4                  |                 |
|                  | <u>Miconia</u> spp. (14 species) | 70                 |                 |
|                  | <u>Clidemia</u> spp.             | 7                  |                 |
| Annonaceae       |                                  | 83                 | 3.03            |
|                  | <u>Xylopia bocatorena</u>        | 23                 |                 |
|                  | <u>Annona</u> spp.               | 9                  |                 |
| Myristicaceae    |                                  | 83                 | 3.03            |
|                  | <u>Dialyanthera otoba</u>        | 24                 |                 |
|                  | <u>Virola</u> spp.               | 24                 |                 |
| Burseraceae      |                                  | 75                 | 2.74            |
|                  | <u>Protium</u> spp.              | 71                 |                 |
|                  | <u>Tetragastris</u> sp.          | 3                  |                 |
| Euphorbiaceae    |                                  | 65                 | 2.37            |
|                  | <u>Mabea occidentalis</u>        | 48                 |                 |
|                  | <u>Richeria</u> spp.             | 8                  |                 |
| Lecythidaceae    |                                  | 62                 | 2.26            |
|                  | <u>Eschweilera pittieri</u>      | 15                 |                 |
|                  | <u>Gustavia dubia</u>            | 11                 |                 |
|                  | <u>Gustavia</u> sp.              | 9                  |                 |
| Myrtaceae        |                                  | 62                 | 2.26            |
|                  | <u>Eugenia</u> spp.              | 22                 |                 |
|                  | <u>Calypttranthes</u> spp.       | 11                 |                 |
|                  | <u>Myrcia</u> spp.               | 6                  |                 |
| Lauraceae        |                                  | 59                 | 2.15            |
|                  | <u>Ocotea cernua</u>             | 5                  |                 |
| Flacourtaceae    |                                  | 43                 | 1.57            |
|                  | <u>Ryania speciosa</u>           | 25                 |                 |
|                  | <u>Carpotroche platyptera</u>    | 8                  |                 |
|                  | <u>Casearia arborea</u>          | 4                  |                 |
| Chrysobalanaceae |                                  | 36                 | 1.31            |
|                  | <u>Licania morii</u>             | 15                 |                 |
|                  | <u>Hirtella trianda</u>          | 6                  |                 |

Table 2--continued.

| Family         | Species | Individuals<br>No. | Percentage<br>% |
|----------------|---------|--------------------|-----------------|
| Anacardiaceae  |         | 25                 | 0.91            |
| Icacinales     |         | 25                 | 0.91            |
| Myrsinaceae    |         | 25                 | 0.91            |
| Boraginaceae   |         | 21                 | 0.77            |
| Meliaceae      |         | 20                 | 0.73            |
| Araliaceae     |         | 19                 | 0.69            |
| Sterculiaceae  |         | 17                 | 0.62            |
| Bignoniaceae   |         | 13                 | 0.47            |
| Elaeocarpaceae |         | 11                 | 0.40            |
| Nyctaginaceae  |         | 11                 | 0.40            |
| Verbenaceae    |         | 11                 | 0.40            |
| Violaceae      |         | 11                 | 0.40            |
| Hippocrataceae |         | 9                  | 0.33            |
| Piperaceae     |         | 7                  | 0.26            |
| Sapindaceae    |         | 7                  | 0.26            |
| Loganiaceae    |         | 6                  | 0.22            |
| Ochnaceae      |         | 6                  | 0.22            |
| Sabiaceae      |         | 6                  | 0.22            |
| Tiliaceae      |         | 6                  | 0.22            |
| Quiinaceae     |         | 5                  | 0.18            |
| Rutaceae       |         | 5                  | 0.18            |
| Ulmaceae       |         | 5                  | 0.18            |

Table 2--continued.

| Family                                         | Species | Individuals<br>No. | Percentage<br>% |
|------------------------------------------------|---------|--------------------|-----------------|
| Caricaceae                                     |         | 4                  | 0.15            |
| Smilacaceae                                    |         | 4                  | 0.15            |
| Erythroxylaceae                                |         | 3                  | 0.11            |
| Polygonaceae                                   |         | 3                  | 0.11            |
| Solanaceae                                     |         | 3                  | 0.11            |
| Monimiaceae                                    |         | 2                  | 0.07            |
| Simaroubaceae                                  |         | 2                  | 0.07            |
| Acanthaceae                                    |         | 1                  | 0.04            |
| Bombacaceae                                    |         | 1                  | 0.04            |
| Chloranthaceae                                 |         | 1                  | 0.04            |
| Dilleniaceae                                   |         | 1                  | 0.04            |
| Humiraceae                                     |         | 1                  | 0.04            |
| Malvaceae                                      |         | 1                  | 0.04            |
| Marcgraviaceae                                 |         | 1                  | 0.04            |
| Olacaceae                                      |         | 1                  | 0.04            |
| Podocarpaceae                                  |         | 1                  | 0.04            |
| Rhizophoraceae                                 |         | 1                  | 0.04            |
| Named                                          |         | 33                 | 1.21            |
| Non-identified or non-collected<br>individuals |         | 711                | 25.97           |
| Total                                          |         | 2738               |                 |

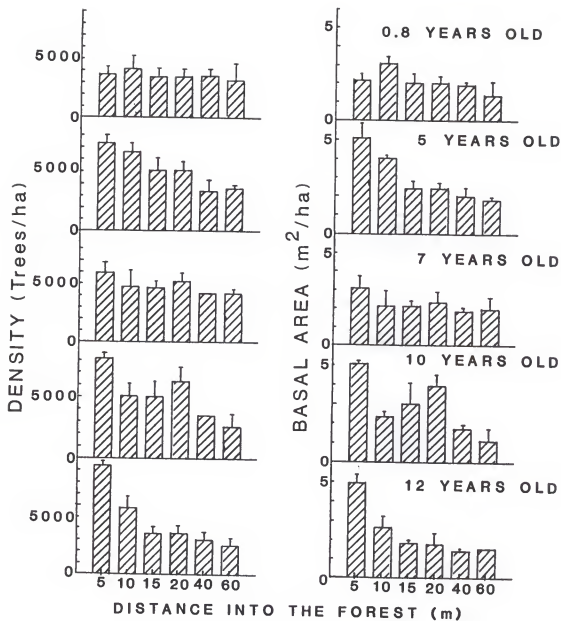


Figure 6. Changes in density (stems/ha) and basal area (m<sup>2</sup>/ha) with distance into the forest for woody plants < 5 cm dbh in the 0.8-, 5-, 7-, 10-, and 12-year-old study sites.

Table 3. The effect of edge age on stem density (no./ha) and basal area ( $m^2$ /ha) at the forest edge (0-20 m) and at the forest interior (20-60 m). Values in parentheses are standard errors. Forest edge values are averages of 16 plots for edges 0.8, 5, 10 and 12 years old and 13 plots for the 7-year-old edge. Forest interior values are averages of 6 point-quarter samples (for trees > 5 cm dbh).

| dbh<br>category<br>(cm) | Edge age<br>(yr) | Stem Density (no./ha) |                     |               |
|-------------------------|------------------|-----------------------|---------------------|---------------|
|                         |                  | Edge<br>0-20 m        | Interior<br>20-60 m | Interior/Edge |
| < 5                     | 0.8              | 3621 (387)            | 3343 (662)          | 0.92          |
|                         | 5                | 6030 (439)            | 3455 (407)          | 0.57          |
|                         | 7                | 5186 (482)            | 4157 (169)          | 0.80          |
|                         | 10               | 6126 (564)            | 3044 (481)          | 0.50          |
|                         | 12               | 5553 (692)            | 2749 (423)          | 0.50          |
| 5 to 9.9                | 0.8              | 709 (94)              | 636 (126)           | 0.90          |
|                         | 5                | 811 (121)             | 782 (102)           | 0.96          |
|                         | 7                | 959 (100)             | 617 (105)           | 0.64          |
|                         | 10               | 1036 (122)            | 676 (38)            | 0.65          |
|                         | 12               | 1086 (167)            | 649 (54)            | 0.60          |
| 10 to 19.9              | 0.8              | 438 (52)              | 356 (24)            | 0.81          |
|                         | 5                | 370 (74)              | 376 (47)            | 1.02          |
|                         | 7                | 478 (68)              | 289 (35)            | 0.60          |
|                         | 10               | 443 (82)              | 506 (71)            | 1.14          |
|                         | 12               | 681 (118)             | 497 (61)            | 0.73          |
| > 20                    | 0.8              | 250 (51)              | 211 (19)            | 0.84          |
|                         | 5                | 312 (58)              | 243 (22)            | 0.78          |
|                         | 7                | 239 (63)              | 202 (23)            | 0.85          |
|                         | 10               | 341 (56)              | 300 (37)            | 0.88          |
|                         | 12               | 285 (53)              | 317 (29)            | 1.11          |

Table 3--extended.

| Basal Area m <sup>2</sup> /ha |                     |               |
|-------------------------------|---------------------|---------------|
| Edge<br>0-20 m                | Interior<br>20-60 m | Interior/Edge |
| 2.30 (0.21)                   | 1.60 (0.35)         | 0.70          |
| 3.45 (0.36)                   | 1.86 (0.21)         | 0.54          |
| 2.44 (0.31)                   | 1.88 (0.27)         | 0.77          |
| 3.55 (0.39)                   | 1.38 (0.35)         | 0.39          |
| 2.77 (0.39)                   | 1.47 (0.06)         | 0.53          |
| 2.96 (0.42)                   | 2.97 (0.64)         | 1.00          |
| 3.24 (0.46)                   | 3.32 (0.47)         | 1.02          |
| 4.04 (0.44)                   | 2.73 (0.46)         | 0.68          |
| 4.31 (0.55)                   | 2.85 (0.17)         | 0.66          |
| 4.39 (0.73)                   | 2.96 (0.24)         | 0.67          |
| 6.30 (0.75)                   | 6.05 (0.56)         | 0.96          |
| 5.09 (1.05)                   | 6.21 (0.91)         | 1.22          |
| 6.89 (1.07)                   | 4.69 (0.54)         | 0.68          |
| 6.46 (1.15)                   | 8.70 (1.24)         | 1.35          |
| 9.20 (1.51)                   | 7.96 (0.92)         | 0.87          |
| 25.03 (7.77)                  | 23.45 (2.90)        | 0.94          |
| 35.74 (8.77)                  | 36.25 (6.81)        | 1.01          |
| 29.89 (8.92)                  | 26.54 (4.89)        | 0.89          |
| 30.70 (6.93)                  | 27.35 (4.56)        | 0.89          |
| 31.82 (7.97)                  | 50.88 (9.68)        | 1.60          |

of trees < 5 cm dbh between 0 and 20 m from the edge; beyond 20 m density and basal area were lower and similar. Trees in the 5-9.9 cm diameter category also showed higher density and basal area between 0 to 20 m from the pasture-forest border than beyond 20 m into the forest on 7-, 10- and 12-year-old sites. Other diameter categories (10-19.9 and > 20 cm dbh), however, did not change in density and basal area with distance into the forest (Table 3).

Stem density of woody plants < 5 cm dbh and > 2 m tall was 49-55% less in the forest interior than at the edge, except for 0.8- and 7-year-old edges (Table 3). Along the 0.8-year-old edge this was a reflection of age. Saplings present when the field was created grew in height, and apparently there was little recruitment from seeds or seedlings.

Based on differences in stem density and basal area for woody plants < 5 cm dbh, and temperature, relative humidity and canopy openness gradients, a "forest edge" was defined as the first 20 m into the forest from the trunk of the trees > 10 cm dbh closest to the pasture. Data from 20 to 60 m from the edge were considered to be representative of the forest interior.

In the forest interior, average density of trees > 10 cm dbh was 659 stems/ha, basal area averaged  $35.9 \text{ m}^2/\text{ha}$ , and canopy height was 30-35 m, with emergent trees 45-50 m tall. From the adjacent clearing, I observed that woody plants < 5 cm dbh formed a very conspicuous layer 5-8 m tall along all edges, except in the youngest edge. Dead branches, however, were observed in the pasture side of tall forest-edge trees.

### Understory Percent Cover

Coverage by plants < 2 m height was sparse but quite uniform with distance into the forest (one-way ANOVA,  $F=2.02$ ,  $F=2.23$ ,  $F=2.63$ ,  $F=0.32$ ,  $F=0.81$ , for 0.8-, 5-, 7-, 10-, and 12-year-old sites, respectively,  $df=5$ ,  $P > .05$ ). The average percent cover was 15.8 ( $n=97$  plots;  $s.d.=5.17$ ). Cover by lifeform was: tree seedlings 4.6%, palms 4.4%, Zingiberales and Araceae 3.2%, ferns 1.4%, herbaceous vines 0.9%, shrubs 0.5%, grasses 0.5%, liana seedlings 0.2%, and herbs 0.1%.

### Lifeforms

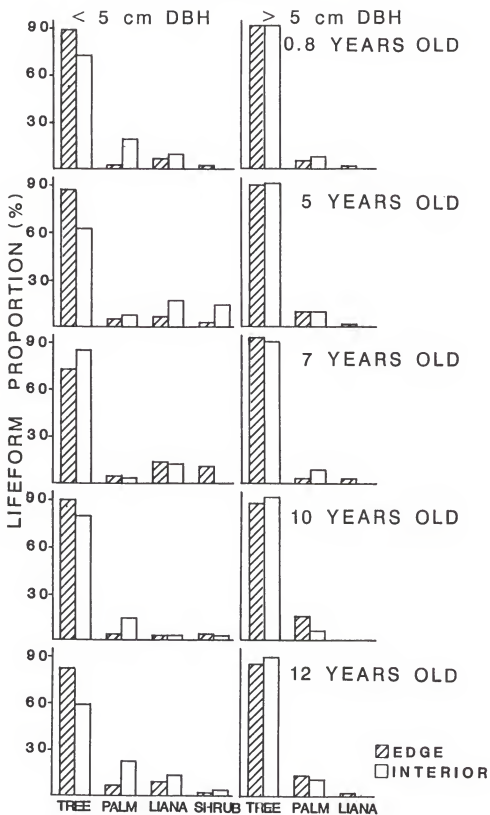
Dicotyledonous trees represented 75-88% of the woody plants < 5 cm dbh and decreased in density with distance into the forest. Palms represented 4 to 5% of all the individuals recorded and increased with distance into the forest along 0.8-, 10-, and 12-year-old edges. Lianas represented 2.8 to 13.0% of all individuals < 5 cm dbh; their abundance did not seem to be related to distance from the edge. Few shrubs were present in forest interiors, except along the 5-year-old edge (Figure 7).

A quite constant tree-to-palm ratio of approximately 9:1 was observed for woody plants > 5 cm dbh in forest interiors and forest edges. Lianas > 5 cm dbh, however, were recorded only on forest edges (Figure 7).

### Effect of Agricultural Practices on Pasture Edge Vegetation

Pasture vegetation near the 5-, 7-, 10-, and 12-year-old forest edges was combined into three groups: planted Ischaemum indicum, herbaceous plants, and woody plants. The most common

Figure 7. Changes in lifeform proportions of woody plants < 5 cm dbh (left) and > 5 cm dbh (right) in the forest edge and in the forest interior of 0.8-, 5-, 7-, 10-, and 12-year-old study sites.



herbs were ferns, Lycopodium sp., sedges, grasses other than I. indicum, and vines belonging to the families Passifloraceae, Rubiaceae, Smilacaceae, and Sapindaceae. The most common woody plants were melastomataceous shrubs, Solanum spp., Vismia macrophylla, Cecropia spp., and Piper spp.

Within 6-10 months, percent cover and height of all the pasture vegetation groups, as well as species composition, changed in the cattle exclusion treatment. They did not, however, vary in the non-exclusion control plots due to cattle grazing and weeding. Percent cover of woody-plants increased and I. indicum decreased ( $t=2.47$ ,  $df=27$   $P=.02$  for ratana;  $t=3.35$ ,  $df=118$ ,  $P=.001$  for woody plants; Figure 8) in the fenced plots in the pasture adjacent to the 10-year-old edges. All vegetation groups in pastures adjacent to the 7-year-old edge ( $t=3.66$ ,  $df=30$ ,  $P=.001$ ;  $t=2.32$ ,  $df=105$ ,  $P=.02$ ;  $t=2.55$ ,  $df=52$ ,  $P=.01$  for ratana, herbs, and woody plants, respectively), and 10-year-old edge ( $t=2.41$ ,  $df=27$ ,  $P=.02$ ;  $t=3.75$ ,  $df=147$ ,  $P < .001$ ;  $t=5.54$ ,  $df=118$ ,  $P < .001$  for ratana, herbs, and woody plants, respectively), as well as herbs ( $t=3.29$ ,  $df=64$ ,  $P=.002$ ) and ratana ( $t=4.82$ ,  $df=22$ ,  $P < .001$ ) in pasture adjacent to the 12-year-old edge, were taller in the fenced plots than in the non-fenced plots. The 5-year-old pasture edge did not differ significantly in cover nor in height between treatments. In all pastures, grazed plots supported fewer species than non-grazed plots.

### Effect of Edge Proximity on Dead Tree Density

Density of dead trees decreased with distance into the forest. Dead trees > 30 cm dbh were 2.6:1 more abundant on edges than in forest interior. The ratio decreased for smaller diameter categories (Figure 9). In the interior, the average density of dead trees > 5 cm dbh was 104 trees/ha. Trees in the forest interior apparently died mainly by snapping (55%), followed by uprooting (33%), and while standing (12%). Most of the dead individuals were dicotyledonous trees (84%); dead palms represented 16% (Table 4). There was no correlation between the density of dead trees and steepness of slope.

Edge and interior dead trees were separated into five decay classes; dead tree density by decay classes differed between edge and interior plots. When the first two classes of least decayed trees were compared the average edge-to-interior ratio for all sites was 14:1 for trees > 5 cm dbh and 15:1 for trees > 10 cm dbh (Table 5). When the last two classes of most decayed trees were used, the number of dead trees at the edge with respect to the interior was roughly 1:1 for trees either > 5 or > 10 cm dbh (Table 5). The greatest edge-to-interior ratio was observed on the 0.8-year-old edge. However, there was not a consistent lessening in the ratio with increase in age edge. The mode of tree death among the trees that died most recently (decay classes 1 and 2) indicated that the edge-to-interior ratios were 14:3, 11:2, and 9:0 for trees that died snapped, uprooted, and standing, respectively. Decay classes are probably biased

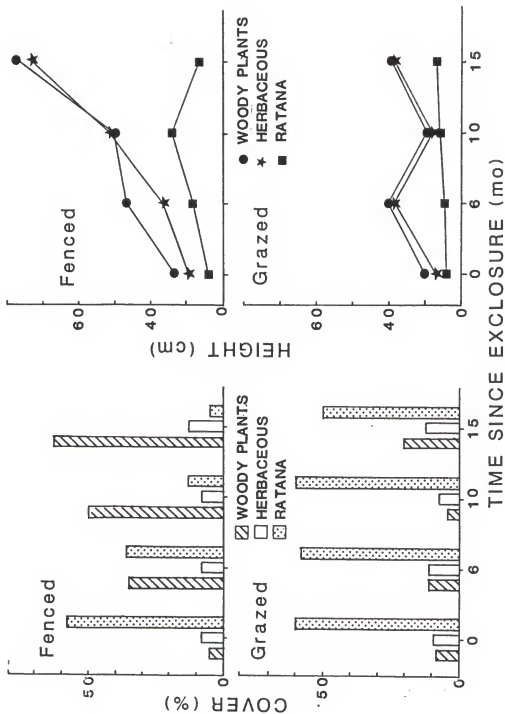


Figure 8. Changes with time in cover (%) and height (cm) of woody plants, herbs, and *Ischaemum rugosum* (ratana grass) in the pasture adjacent to the 10-year-old study site in fenced (above) and grazed (below) plots.

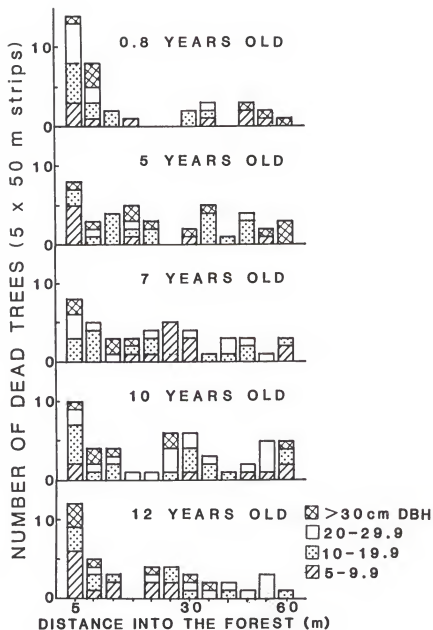


Figure 9. Number of dead trees in 5 x 50 m strips parallel to the forest edge for 0.8-, 5-, 7-, 10-, and 12-year-old study sites. Diameter categories are dead trees 5-9.9, 10-19.9, 20-29.9, and > 30 cm dbh.

Table 4. Number of dead woody plants > 5 cm dbh in 0.2 ha plots, apparent mode of death, and lifeform in the forest interior (20-60 m into the forest).

| dbh<br>category<br>(cm) | Edge age<br>(yr) | Total<br>No. | Mode of death |        |       | Lifeform |      |
|-------------------------|------------------|--------------|---------------|--------|-------|----------|------|
|                         |                  |              | Snap          | Uproot | Stand | Tree     | Palm |
| < 5                     | 0.8              | 11           | 4             | 4      | 3     | 9        | 2    |
|                         | 5                | 20           | 11            | 7      | 2     | 17       | 3    |
|                         | 7                | 24           | 13            | 6      | 5     | 15       | 9    |
|                         | 10               | 29           | 20            | 8      | 1     | 27       | 2    |
|                         | 12               | 20           | 9             | 9      | 2     | 19       | 1    |
|                         | Mean             | 21           | 11            | 7      | 3     | 17       | 3    |
| 5 to 9.9                | 0.8              | 4            | 2             | 1      | 1     | 3        | 1    |
|                         | 5                | 2            | 1             | 1      | 0     | 2        | 0    |
|                         | 7                | 11           | 4             | 4      | 3     | 7        | 4    |
|                         | 10               | 5            | 4             | 1      | 0     | 4        | 1    |
|                         | 12               | 4            | 2             | 2      | 0     | 4        | 0    |
|                         | Mean             | 5            | 3             | 2      | 1     | 4        | 1    |
| 10 to 19.9              | 0.8              | 3            | 1             | 1      | 1     | 2        | 1    |
|                         | 5                | 10           | 8             | 1      | 1     | 7        | 3    |
|                         | 7                | 7            | 4             | 1      | 2     | 3        | 4    |
|                         | 10               | 13           | 8             | 4      | 1     | 12       | 1    |
|                         | 12               | 7            | 4             | 3      | 0     | 6        | 1    |
|                         | Mean             | 8            | 5             | 2      | 1     | 6        | 2    |
| > 20                    | 0.8              | 4            | 1             | 2      | 1     | 4        | 0    |
|                         | 5                | 8            | 2             | 5      | 1     | 8        | 0    |
|                         | 7                | 6            | 5             | 1      | 0     | 5        | 1    |
|                         | 10               | 11           | 8             | 3      | 0     | 11       | 0    |
|                         | 12               | 9            | 3             | 4      | 2     | 9        | 0    |
|                         | Mean             | 8            | 4             | 3      | 1     | 7        | 0    |

Table 5. Number of dead trees/ha by decay classes on the forest edge (0-20 m) and in the forest interior (20-60 m). Class 1 is the least decayed and class 5 is the most decayed (see text for further description).

| dbh<br>category<br>(cm) |          | Decay<br>classes | Edge age (yr) |     |     |     |    | Mean |
|-------------------------|----------|------------------|---------------|-----|-----|-----|----|------|
|                         |          |                  | 0.8           | 5   | 7   | 10  | 12 |      |
| > 5                     | Edge     | 1 & 2            | 120           | 60  | 60  | 20  | 80 | 68   |
|                         | Interior | 1 & 2            | 0             | 5   | 15  | 5   | 0  | 5    |
|                         | Edge     | 4 & 5            | 80            | 120 | 120 | 110 | 70 | 100  |
|                         | Interior | 4 & 5            | 40            | 85  | 65  | 125 | 90 | 81   |
|                         | Edge     | 1 & 2            | 80            | 30  | 50  | 20  | 40 | 44   |
|                         | Interior | 1 & 2            | 0             | 5   | 5   | 5   | 0  | 3    |
| > 10                    | Edge     | 4 & 5            | 80            | 90  | 120 | 110 | 30 | 86   |
|                         | Interior | 4 & 5            | 25            | 75  | 40  | 105 | 70 | 63   |

because woody decay rates are species-specific and depend on bole diameter (Lang and Knight 1979, Harmon 1982). Nevertheless, when decay classes were not considered, average density of dead trees along all forest edges was 206 trees/ha, which is twice the average density found in the forest interior. These results strongly suggest that there is an increase in tree mortality when an edge is created.

### Discussion

Beyond 20 m into the forest from the pasture-forest border, environmental and structural variables were apparently not influenced by proximity to the edge. The definition of a forest edge, however, depends upon the organisms under consideration. There is some evidence that edges affect animals farther into the forest than plants. For instance, studies on bird-nest predation showed an edge effect that extended as far as 200-500 m into the forest (Wilcove et al. 1986, Andrén and Angelstam 1988), but Gates and Gysel (1978) found that edge effect on bird-nest predation extended only 45 m into the forest. Studies of plants in temperate-zone deciduous forest, on the other hand, indicate that the edge effect on basal area, stem density, and leaf area density extends only 10-15 m beyond the clearing (Ranney et al. 1981, Miller and Lin 1985).

Edge effects on microenvironment variables reaches different distances into the forest, depending on edge age due to development of edge vegetation. At my study sites, a marked change in environmental conditions occurred within 2.5-15 m of

the clearing-forest border, although the change was less abrupt in the 7-year-old edge than in younger and older ones. Temperature, relative humidity, and canopy openness beyond 15-25 m into the forest were similar to other tropical wet forests remote from edges. Microenvironmental differences along transects agree with reports that maximum and minimum temperatures are higher, and relative humidity is lower in clearings and clearing-forest borders than in tropical forest interiors (Schulz 1960, Grubb and Whitmore 1966, Lawson et al. 1970, Longman and Jenik 1974, Thompson and Pinker 1975, Lawson et al. 1981, Lovejoy et al. 1986).

Altered microclimatological conditions resulting from forest clearance affect edge vegetation structure. For instance, edges older than 5 years (except 7-year-old edge) support twice the density of woody plants  $< 5$  cm dbh in the 20 m closest to the clearing than in the forest interior. These results are similar to reports from temperate deciduous forest edges, where edge values of stem density were around 200% higher than interior densities (Ranney et al. 1981). The youngest edge I studied had vegetation similar to that of the forest interior, apparently because 10 months is too little time to develop edge vegetation structure. The 7-year-old edge had also lower density and basal area than expected, which can be related to a relatively flat topography. Within 5 years, however, most edge vegetation developed a wall of woody plants that insulated the forest from conditions of the clearing.

The wall of vegetation was mostly composed of tree saplings and palms. Contrary to expectation, lianas < 5 cm dbh showed a similar proportion of plants along edges as in the forest interior. Lianas > 5 cm diameter, however, were recorded only along edges. This contrasts with observations that liana seedlings are abundant and grow significantly taller along gap edges than in the gap center and the forest interior (Putz 1984). Possibly due to increased lateral light penetration, lianas present before edge creation grew in diameter and length without increasing numerically.

Increased mortality rates of edge trees are probably related to drastic changes in microenvironmental conditions. In the 5-m band closest to the edge the number of dead trees was greatest. Farther than 15-20 m into the forest the number of dead trees was lowest and similar to forest interior. Furthermore, tree death modes along edges differ in proportion with respect to forest interior. In the forest edge the number of trees that died standing was higher than in the interior. The ways in which trees died in the forest interior were similar to those observed on Barro Colorado Island (BCI, Panama), where most dead trees had snapped and smaller proportions had been uprooted or had died standing (Putz and Milton 1982). Dicotyledonous trees and palms were equally likely to die when an edge was created in their proximity. Trees from higher diameter categories, however, died in a higher proportion along edges than in forest interior. The increased number of dead trees and the fact that more trees died standing at the edge than in the forest interior is a reflection

of the environmental stress experienced by trees isolated from the protection of neighboring vegetation (Lovejoy et al. 1986, Waring 1987, Hubbell and Foster 1988, Lawton and Putz 1988).

Altered vegetation structure and increased rates of tree mortality confer a peculiar physiognomy on forest edges. Observed from the pasture side, forest edge vegetation consisted of a well-defined 5-8 m tall layer of understory woody vegetation and tall trees. These two vegetation layers were easily distinguished. Crowns of the < 8 m tall layer of woody plants were growing toward the clearing. However, crowns of tall edge-forest trees were growing away from the clearing, and branches were dead on the clearing side. Dead crowns of tall trees apparently contrast with observations, from the temperate zone, of lateral growth of crowns toward canopy gaps and artificially created forest edges (Gysel 1951, Trimble and Tryon 1966, Levenson 1981, Ranney et al. 1981, Hibbs 1982, Runkle 1982). In high altitude forest of Abies balsamea, however, death of trees located in an exposed front is common (Sprugel 1976, Sprugel and Bormann 1981). Also, in Central Amazonia dead trees are abundant along forest edges (Lovejoy et al. 1984). The prevalence of dying trees along tropical forest edges (and high-altitude temperate forest) suggests that environmental conditions are much more severe on tropical forest edges than on temperate forest edges with respect to forest interior, or that tropical forest-grown trees are less adaptable to new environmental conditions when isolated from neighboring vegetation.

Edge vegetation development is faster in tropical forest than in temperate forest. The understory vegetation layer was well-developed within 5 years of edge creation with twice the edge stem density and basal area than the forest interior. On temperate deciduous forest edges, on the other hand, stem density and leaf density require about 20 years to be twice as large at the edge as in the forest interior (Ranney et al. 1981, Miller and Lin 1985).

Plant species composition on forest edges and in the forest interior consisted mostly of shade-tolerant species with few light-demanding species. Tropical forests present a continuum of regeneration patterns (Augsburger 1984, Brokaw 1987, Hubbell and Foster 1987), but for convenience, tree species are clumped into a few regeneration groups. Two common classes are primary and secondary, or light-demanding and shade-tolerant species (Whitmore 1975). The shade-tolerant species persist as suppressed seedlings or saplings in the understory until a canopy gap opens above or near them and permits accelerated growth (Brokaw 1987). The light-demanding species germinate in gaps and grow rapidly. These species can rarely be found growing in the forest understory, except perhaps under deciduous trees or close to gaps (Hubbell and Foster 1987).

Although edge vegetation was expected to be dominated by light-demanding plants, this turned out not to be the case. The floristic composition, in general, was similar at edge and forest interior with mostly shade-tolerant species. Light-demanding species were abundant in intended contiguous pastures, but in the

adjacent forest they were mostly growing in light gaps. In temperate deciduous forest, in contrast, species composition often differs markedly between edges and interiors. Edges are more species rich, and shade-intolerant species are abundant along forest edges (Wales 1972, Ranney et al. 1981). Likewise, abundant regrowth of light-demanding species is observed along tropical forest edges in Central Amazonia (Lovejoy et al. 1984). The scarcity of light-demanding plants on forest edges I studied in Panama indicates that besides increased light penetration, secondary species have other requirements for germination and establishment (see Chapter IV). Quality of light (Vázquez-Yanes and Smith 1982, Vázquez-Yanes and Orozco-Segovia 1985) and soil disturbance (Wesson and Wareing 1969, Bell 1970, Putz 1983) may influence the presence of pioneer species in forest edges. Also, the faster growth of preexisting plants in tropical forest edges than in temperate deciduous forest may curtail the establishment of light-demanding species.

When cattle were excluded from pastures adjacent to forest edges, the general effect was a drastic reduction of pasture grass and an increase in number, percent cover, and height of woody plants. Studies comparing grazed and ungrazed vegetation have usually found that species diversity is higher in moderately grazed areas (Harper 1977, Collins 1987). Other authors, however, have reported that species diversity decreases as a function of increasing grazing by cattle (Waser and Price 1981), other large mammals (Belsky 1986), and small mammals (Dickinson and Kirkpatrick 1986). In my study, the fenced plots had higher

number of species than unfenced plots, and the pasture grass was shaded by woody species within 6-10 months. In the unfenced plots woody plants were browsed or cut when pastures were maintained. An implication of these observations is that sharp pasture-forest edges are a result of grazing and pasture maintenance.

This study shows how edge vegetation structure changes with both distance into the forest and time. When edges are created, microenvironmental conditions in forest close to the pasture margin are much modified. Density, basal area, and tree mortality increase in response to changes in temperature, relative humidity, canopy openness, and presumably reduction in below-ground competition. Higher tree mortality and penetration of lateral light stimulate the forest near the edge to develop higher densities of woody plants than the forest interior. Edge vegetation in my study area is composed mostly of shade-tolerant plants. Increased density of edge plants with time will compensate high tree mortality, if the forest remains undisturbed and the pasture-forest border is maintained through agricultural practices.

## CHAPTER IV THE ORIGIN OF EDGE VEGETATION

### Introduction

Different functional responses to abiotic environmental conditions among plant species and among lifeforms may determine whether they are well-represented on edges. For instance, on gap edges climbing lianas are more numerous than in gap centers and forest interior, partially because of the abundance of support provided by tree proliferation (Putz 1984). On gap edges, understory palms have higher rates of leaf production and height growth than seedlings of similar age grown in the closed canopy, presumably because light intensity is optimal on edges (Chazdon 1986). There is some evidence that shade-tolerant tree species regenerate primarily in small gaps and on the edges of large gaps (Barton 1984). Despite its potential importance in forest conservation, edge vegetation is little studied. It is known, however, that vegetation structure differs between forest edge and forest interior, but floristic composition is not necessarily different (Chapter III). The underlying working hypothesis in this part of my investigation is that species composition of edge plants depends on the origin of these plants.

Newly opened forest edges presumably have soil seed bank compositions similar to those of undisturbed forest from the same region. With time, the forest edge soil seed bank is expected to

change due to input of new propagules, seed predation, and germination of seeds in response to light penetration. Soil seed banks of primary tropical forests contain large numbers of secondary species (e.g., Guevara and Gómez-Pompa 1972, Putz 1983, Hopkins and Graham 1983, Enright 1985). The structure and composition of the vegetation that develops after disturbance depends in part on the germination of these seeds. A reduction of canopy density increases the red:far-red ratio of incident light, which triggers the germination of pioneer tree seeds under photocontrol, such as Cecropia obtusifolia, Heliocarpus donnell-smithii and Piper auritum (Vázquez-Yanes and Orozco-Segovia 1985). Germination, however, is markedly lower in small gaps and towards the periphery of large gaps than on clearings where direct sunlight reaches the forest floor during longer periods (Vázquez-Yanes 1980, Vázquez-Yanes and Smith 1982).

Soil disturbance, even if not an inevitable consequence of edge creation, has been reported as an important agent in seed germination. Soil disturbance was observed to be a critical factor for germination of some secondary species such as Phytolacca icosandra in a tropical rainforest in Puerto Rico (Bell 1970). Also, in the forest on Barro Colorado Island (BCI, Panama) pioneer trees were more concentrated on the soil disturbed by uprooted trees than elsewhere in treefall gaps (Putz 1983). In cultivated land, the number of viable seeds declines rapidly after soil disturbance due to germination (Roberts and Feast 1973). Therefore, the appearance of weed seedlings depends

on exposure (through soil disturbance) of buried seeds to light (Wesson and Wareing 1969).

When an edge is created, part of the forest canopy is removed. Sprouts and seedlings on the forest floor are forced to cope with an environment that has been abruptly modified (Lee 1978, Chapter III). Some seedlings of shade-tolerant species, when exposed to open conditions, develop sun-burned and necrosed leaves (Lovejoy et al. 1983, Fetcher et al. 1987). Similarly, understory palms grown under light conditions of a large gap center show bleached foliage, reduced quantum yield, and reduced light-saturated photosynthetic rates (Chazdon 1986). Seedlings present on the forest floor may respond vigorously when a gap forms. Many forest floor tree seedlings, however, die as a consequence of canopy removal (Liew and Wong 1973, Uhl 1982).

Seedlings on forest edges are not exposed to direct sun all day long, but the influence of the adjacent clearing can be reflected in seed germination, survival and mortality of seedlings, seedling height growth, and eventual formation of a forest edge vegetation structurally different from forest interior vegetation (Fetcher et al. 1983, 1987, Brokaw 1985b, Lovejoy et al. 1986, Chazdon 1986, Clark 1988). Differences in growth rate between light-demanding and shade-tolerant trees can influence their relative abundance on forest edges. Growth rate, however, is rapid only in relation to availability of resources, for example, light intensity (Canham and Marks 1985).

### Methods

This section of my research on forest edge development was motivated by several questions. Why are light-demanding tree species rare at the forest edges that I studied (see Chapter III)? What is the origin of edge plants? Are they coming from the soil seed bank, or from seedlings and saplings present before the edge was created? The study was carried out in an experimental edge described in Chapter II.

#### Soil Seed Bank along the Future Edge

To estimate the population of viable seeds in the soil, before forest edge creation twelve soil samples were collected at randomly selected locations along the future edge. Fresh litter was removed from the soil surface, and 30 x 30 cm, 5 cm deep soil samples were collected. The samples were moved to a screened growing house in Panama City and spread in 50 x 30 cm trays. Two soil samples were autoclaved and used as controls to detect contamination by seed entry into the growing house. Trays were watered daily during the 3-month period of monitoring seedling emergence; identified seedlings were removed from the trays to reduce shade. Unidentified seedlings were transplanted and grown until identification became possible. Vouchers were deposited in the University of Panama Herbarium.

#### Seed Germination in Response to Canopy Opening

To determine the effects of clearcutting the forest on canopy openness in the resulting edge, canopy photographs were taken using a fish-eye lens placed at 60 cm above the ground at

eight randomly selected points along the edge before it was created and immediately after the forest was clearcut. The negatives were analyzed for percent canopy cover using a canopy photo analysis system designed by Becker et al. (unpub.).

To determine if increased radiation resulting from forest felling could promote germination of light-sensitive seeds, bioassays were carried out with two species known to have light-sensitive seeds. The two species used were Paulownia tomentosa, a light-sensitive temperate zone species, and Phytolacca rivinoides, a native species, common in early secondary successional sites. Percent viability for both species was determined in Panama City before starting field experiments. In the P. tomentosa bioassay, Petri plates were placed every 2 m along 4 transects from 10 m out in the clearing to 20 m into the forest. Due to unavailability of viable P. rivinoides seeds, Petri plates were placed only every 5 m along two transects from 10 m out in the clearing to 10 m into the forest. Each Petri plate contained 50 seeds; the seeds were kept moist for the entire experimental period.

#### Seed Germination in Response to Soil Disturbance

To determine if soil disturbance promotes germination of buried seeds, five 1 x 1 m plots were laid out along the newly created edge interspersed among plots in which growth of the advance regeneration was recorded (see below); these undisturbed-soil plots served as controls. The fresh litter and all existing plants (seedlings and herbs) were removed from the surface. The

soil was disturbed to a depth of 5 cm by plowing it with machete and rake. Species, number of individuals, and maximum height were recorded eight months after disturbance.

#### Height Growth of Advance Regeneration

To determine the response of seedlings and saplings (<2 m tall) present before edge creation to an increase in canopy opening, permanent plots were marked along the future forest edge. Eight 2 x 2 m plots were established at random locations along the future edge and another 8 were established 20 m into the forest from the edge. In each plot, all woody plants 8-200 cm tall were tagged and their height recorded. The plots at the edge were inventoried before the forest was cut. After the forest was cut, recruitment, mortality, and growth of plants were recorded in all the plots in March, and at 6-8 week intervals until November. Relative growth rates of seedlings and saplings present in edge and interior plots during the nine-month period of monitoring were calculated following procedures described by Evans (1972).

#### Results

##### Soil Seed Bank along the Future Edge

Seed germination from the soil bank was high. Secondary forest species were well represented. After 3 months a mean of 937 seeds/m<sup>2</sup> germinated (Table 6). Most of the germinated seeds were woody plants (70.2%), followed by herbaceous dicots (12.1%), vines (0.6%), and Zingiberales (0.6%).

Table 6. Species composition and number of germinated seeds in the soil bank from undisturbed primary forest.

|                    | TRAY NUMBER |     |     |     |     |      |      |      |      |      |                      |
|--------------------|-------------|-----|-----|-----|-----|------|------|------|------|------|----------------------|
| Species            | 1           | 2   | 3   | 4   | 5   | 6    | 7    | 8    | 9    | 10   | Total                |
| <u>Piper spp.</u>  | 7           | 11  | 11  | 4   | 7   | 26   | 17   | 22   | 26   | 28   | 159                  |
| Miconia spp.       | 9           | 12  | 24  | 4   | 4   | 34   | 16   | 15   | 20   | 6    | 144                  |
| Cecropia spp.      | 16          | 21  | 6   | 3   | 6   | 28   | 18   | 9    | 21   | 11   | 139                  |
| Compositae         | 8           | 6   | 7   | 15  | 4   | 13   | 11   | 6    | 15   | 12   | 97                   |
| Euphorbiaceae      | 0           | 0   | 11  | 0   | 7   | 1    | 2    | 16   | 10   | 7    | 54                   |
| Solanum spp.       | 7           | 3   | 3   | 1   | 0   | 6    | 7    | 7    | 2    | 11   | 47                   |
| Trema micrantha    | 0           | 3   | 2   | 2   | 4   | 3    | 7    | 1    | 1    | 7    | 30                   |
| Jacaranda sp.      | 1           | 5   | 1   | 0   | 0   | 1    | 0    | 0    | 1    | 1    | 10                   |
| Chenopodiaceae     | 0           | 0   | 1   | 1   | 0   | 0    | 2    | 1    | 0    | 0    | 5                    |
| Cissus sp.         | 0           | 3   | 0   | 0   | 0   | 1    | 0    | 0    | 0    | 0    | 4                    |
| Heliconia spp.     | 0           | 1   | 1   | 0   | 0   | 1    | 0    | 0    | 0    | 1    | 4                    |
| Zanthoxylum sp.    | 0           | 1   | 0   | 0   | 0   | 1    | 0    | 0    | 1    | 1    | 3                    |
| Urticaceae         | 0           | 0   | 1   | 0   | 0   | 1    | 1    | 0    | 0    | 0    | 3                    |
| Apeiba membranacea | 0           | 1   | 0   | 0   | 0   | 0    | 0    | 0    | 1    | 0    | 2                    |
| Blechnum sp.       | 0           | 0   | 0   | 0   | 0   | 0    | 0    | 1    | 0    | 0    | 1                    |
| Passiflora sp.     | 0           | 0   | 0   | 1   | 0   | 0    | 0    | 1    | 0    | 1    | 1                    |
| Alchornea sp.      | 0           | 0   | 0   | 0   | 0   | 0    | 0    | 0    | 0    | 0    | 1                    |
| Costus sp.         | 0           | 0   | 0   | 0   | 0   | 1    | 0    | 0    | 0    | 0    | 1                    |
| Psychotria sp.     | 1           | 0   | 0   | 0   | 0   | 0    | 0    | 0    | 0    | 0    | 1                    |
| Tetrorchidium sp.  | 0           | 0   | 0   | 1   | 0   | 0    | 0    | 0    | 0    | 0    | 1                    |
| Carludovica sp.    | 0           | 0   | 0   | 0   | 0   | 0    | 0    | 1    | 0    | 0    | 1                    |
| Flacourtiaceae     | 0           | 0   | 0   | 0   | 0   | 0    | 1    | 0    | 0    | 0    | 1                    |
| Monocots           | 0           | 0   | 3   | 0   | 7   | 19   | 8    | 13   | 14   | 1    | 65                   |
| Other species      | 7           | 8   | 10  | 9   | 5   | 11   | 3    | 3    | 2    | 10   | 68                   |
| Total              | 56          | 75  | 81  | 41  | 44  | 146  | 93   | 95   | 16   | 96   | 843                  |
| No./m <sup>2</sup> | 622         | 833 | 900 | 456 | 489 | 1622 | 1033 | 1056 | 1289 | 1067 | Mean 937<br>s.d. 362 |

### Seed Germination in Response to Canopy Opening

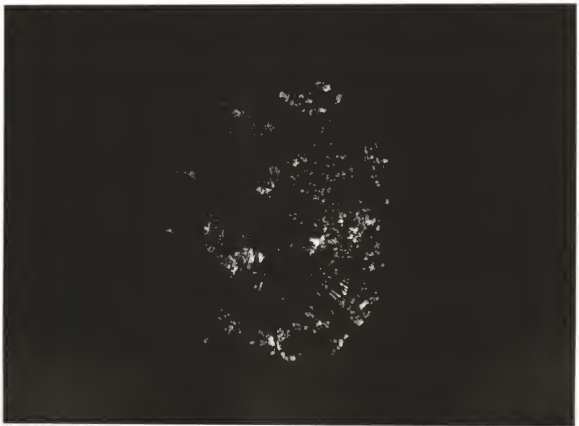
The average canopy openness of undisturbed forest was 1.0% (s.d.=0.62; n=8). After edge creation, canopy openness increased to 16.5% (s.d.=1.64; n=8;  $t=25.1$ ;  $P < .001$ ) under the forest edge canopy, 1.0 m into the forest (Figure 10).

Results of the Paulownia tomentosa bioassay were unexpected in the sense that seeds placed in the clearing and forest interior did not germinate, but seeds on the forest edge did (Figure 11). On the other hand, Phytolacca rivinoides seeds placed in the clearing germinated (80-90%) but seeds placed 2-10 m into the forest did not. Under the forest edge canopy, 1 m from the clearing border, however, 100% of the seeds germinated (Figure 11). Paulownia tomentosa seeds had a very low germination percentage (10%) both in laboratory test and bioassay, and P. rivinoides had a very high germination (100%).

### Seed Germination in Response to Soil Disturbance

Soil disturbance treatment clearly influenced seedling density and floristic composition. The average number of germinated seeds in the disturbed soil plots was  $154/m^2$  (s.d.=72.5; range 71-265 plants; n=5; Table 7). Species composition in the soil disturbance experiment was similar to the floristic composition in the soil seed bank study. Woody plants represented 49.5% of all individuals, vascular cryptogams (ferns and Selaginella) 38.1%, herbaceous dicots 3.6%, Zingiberales (including members of the Marantaceae and Musaceae) 1.8%, and vines 0.4%. Maximum height of herbaceous vines was 60 cm, woody

Figure 10. Canopy photographs before (below) and after (above) the edge was created in the experimental site.



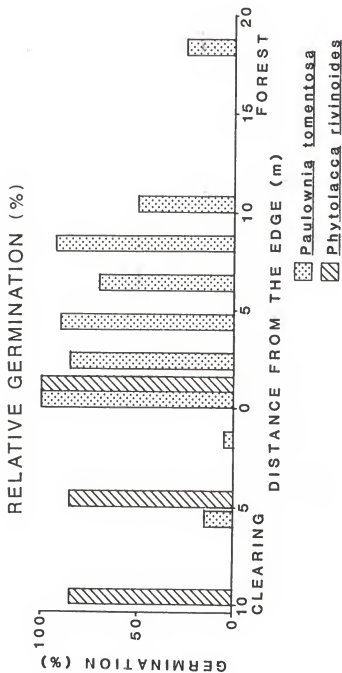


Figure 11. Relative germination percent of *Paulownia tomentosa* and *Phytolacca rivinoides* bioassays along transects from 10 m out in the clearing to 20 m into the forest in the experimental site.

Table 7. Species composition and number of germinated seeds in response to the soil disturbance treatment in 1 x 1 m plots along the forest edge.

| Species                 | Plots |    |     |     |     | Total<br>No. |
|-------------------------|-------|----|-----|-----|-----|--------------|
|                         | 1     | 2  | 3   | 4   | 5   |              |
| <u>Pityrogramma</u> sp. | 100   | 0  | 21  | 52  | 109 | 282          |
| <u>Cecropia</u> spp.    | 29    | 19 | 54  | 16  | 34  | 152          |
| <u>Piper</u> spp.       | 6     | 19 | 36  | 8   | 55  | 124          |
| <u>Miconia</u> sp. 1    | 7     | 7  | 0   | 19  | 31  | 64           |
| Compositae              | 7     | 14 | 1   | 1   | 5   | 28           |
| <u>Carludovica</u> sp.  | 5     | 3  | 7   | 5   | 6   | 26           |
| <u>Heliconia</u> spp.   | 1     | 0  | 3   | 2   | 4   | 10           |
| <u>Polypodium</u> sp.   | 0     | 1  | 0   | 0   | 7   | 8            |
| <u>Miconia</u> sp. 2    | 0     | 0  | 0   | 7   | 1   | 8            |
| <u>Solanum</u> sp.      | 3     | 1  | 1   | 1   | 1   | 7            |
| <u>Miconia</u> sp. 3    | 1     | 0  | 1   | 1   | 2   | 5            |
| Solanaceae              | 1     | 1  | 0   | 1   | 1   | 4            |
| Marantaceae             | 0     | 0  | 0   | 4   | 0   | 4            |
| <u>Zanthoxylum</u> sp.  | 2     | 0  | 1   | 0   | 1   | 4            |
| <u>Passiflora</u> sp.   | 0     | 1  | 0   | 2   | 0   | 3            |
| <u>Selaginella</u> sp.  | 0     | 0  | 1   | 2   | 0   | 3            |
| <u>Jacaranda</u> sp.    | 2     | 1  | 0   | 0   | 0   | 3            |
| <u>Costus</u> sp.       | 1     | 0  | 0   | 1   | 1   | 3            |
| <u>Miconia</u> sp. 4    | 1     | 0  | 0   | 0   | 2   | 3            |
| <u>Trema micrantha</u>  | 1     | 0  | 1   | 0   | 0   | 2            |
| Annonaceae              | 1     | 1  | 0   | 0   | 0   | 2            |
| Cyperaceae              | 0     | 0  | 0   | 0   | 1   | 1            |
| Rubiaceae               | 0     | 0  | 0   | 1   | 0   | 1            |
| <u>Protium</u> sp.      | 1     | 0  | 0   | 0   | 0   | 1            |
| <u>Solanum tortum</u>   | 1     | 0  | 0   | 0   | 0   | 1            |
| Other species           | 7     | 3  | 3   | 4   | 4   | 21           |
| Total                   | 177   | 71 | 130 | 127 | 265 | 770          |
| No./m <sup>2</sup>      |       |    |     |     |     | 154          |
| s.d.                    |       |    |     |     |     | 72.5         |

plants 30 cm, Zingiberales 23 cm, herbaceous dicots 21 cm, and ferns 20 cm.

After 8 months, the disturbed soil plots had 10 times more seedlings/m<sup>2</sup> of woody plants (76 individuals/m<sup>2</sup>; s.d.=34.1; n=5) than undisturbed soil plots. Cecropia spp. represented 40% of the woody plants in the disturbed soil plots, while Piper spp. represented 33%, and Miconia spp. 21%.

#### Height Growth of Advance Regeneration

Seedlings present prior to forest clearing grew faster by a factor of 2 on the forest edge than 20 m into the forest ( $t=5.349$ ;  $P < .001$ ). Relative growth rates over the 8 month observation period were 0.029 cm/cm/mo (s.d.=0.031; n=191 plants) for edge plants and 0.014 cm/cm/mo (s.d.=0.015; n=147 plants) for interior plants. Absolute growth rates were 0.9 cm/mo (s.d.=1.10; n=191 plants) and 0.4 cm/mo (s.d.=0.39; n=161) for edge and interior plants, respectively. Edge plants grew faster than interior plants both during the first month following edge creation ( $t=2.397$ ;  $P=.017$ ) and during the 6-9 month period of monitoring ( $t=2.904$ ;  $P=.004$ ).

Seedling density and recruitment were higher on the forest edge than in the forest interior (Figures 12 and 13). During the whole study period, recruitment varied in a range of 6.5 to 8.5 seedlings/m<sup>2</sup> and total density increased by one seedling/m<sup>2</sup> on the forest edge, whereas in the forest interior recruitment varied from 0.5 to 4.0 seedlings/m<sup>2</sup> and density remained constant.

Seedling survival was lower for edge plants (77.6%) than for forest interior plants (84.3%) during the first 7 months

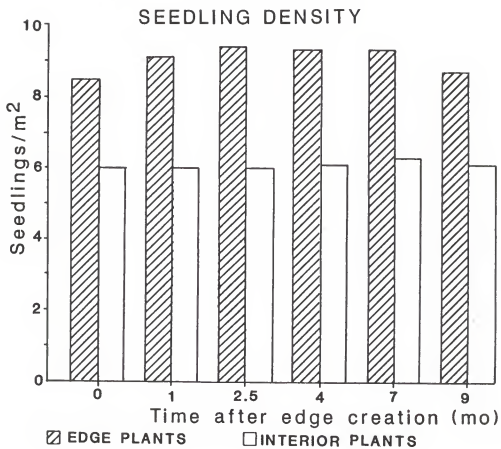


Figure 12. Seedling density on the forest edge and 20 m into the forest interior in the experimental site.

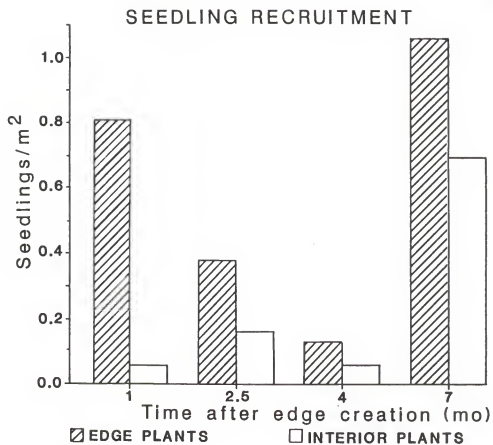


Figure 13. Seedling recruitment on the forest edge and 20 m into the forest in the experimental site.

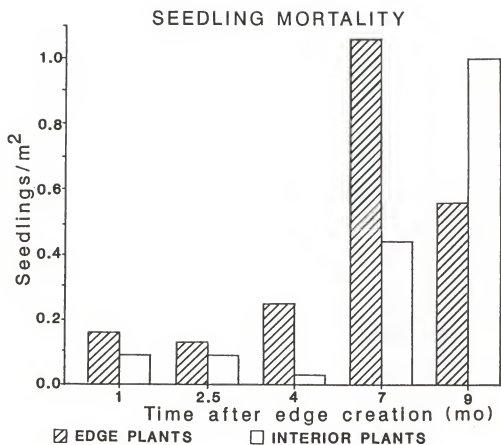


Figure 14. Seedling mortality on the forest edge and 20 m into the forest in the experimental site.

following edge creation. By the end of the monitoring period (7-9 months), a large branch had fallen on a forest interior plot, destroying all tagged plants and making survivorship (77.0%) similar to forest edge (Figure 14).

Floristic composition was similar in forest edge and forest interior plots (Table 8). Most individuals were shade-tolerant; very few individuals of light-demanding species were recorded. For instance, Cecropia spp. represented 0.9% of all forest edge plants and 1.8% of forest interior plants; Piper spp. constituted 1.4% of edge plants and 0.4% of interior plants, and Melastomataceae constituted 0.9% of edge plants and 0% of interior plants. Woody plants represented 52.1% of edge plants and 54.3% of interior identified plants. Vines and lianas represented 2.6% of all edge plants and 3.1% of all interior plants.

### Discussion

When the forest edge was created, seeds of light-demanding woody species were numerically well represented in the soil bank. Seed density in the soil bank was high but in the range of values reported for several undisturbed tropical forests (Guevara and Gómez-Pompa 1972, Uhl 1982, Putz 1983, Hopkins and Graham 1983, Enright 1985, Lawton and Putz 1988). Germination of these seeds is promoted by removal of the forest canopy and soil disturbance (Putz 1983, Whitmore 1983). If the canopy openness is partial, for instance in a small light gap or edges of large gaps, germination is low and saplings present before canopy opening quickly fill the space (Vázquez-Yanes 1980, Brokaw 1985b).

Table 7. Species composition and number of woody plants (< 2 m tall) on forest edge and forest interior 2 x 2 m plots.

| Species                     | Location |          | Total |
|-----------------------------|----------|----------|-------|
|                             | Edge     | Interior |       |
| <u>Brosimum</u> sp.         | 83       | 48       | 131   |
| Leguminosae                 | 22       | 10       | 32    |
| <u>Quassia</u> sp.          | 13       | 19       | 32    |
| Moraceae                    | 7        | 5        | 12    |
| Sapotaceae                  | 7        | 3        | 10    |
| <u>Dipteryx</u> sp.         | 6        | 4        | 10    |
| Rubiaceae                   | 5        | 5        | 10    |
| <u>Copaifera panamensis</u> | 5        | 2        | 7     |
| <u>Cecropia</u> sp.         | 3        | 4        | 7     |
| Guttiferae                  | 0        | 7        | 7     |
| Piperaceae                  | 5        | 1        | 6     |
| <u>Faramea</u> sp.          | 5        | 1        | 6     |
| Chrysobalanaceae            | 5        | 0        | 5     |
| Menispermaceae              | 2        | 2        | 4     |
| <u>Inga</u> spp.            | 1        | 3        | 4     |
| Nyctaginaceae               | 4        | 0        | 4     |
| Annonaceae                  | 0        | 3        | 3     |
| <u>Chrysophyllum</u> sp.    | 0        | 3        | 3     |
| <u>Aspidosperma</u> sp.     | 3        | 0        | 3     |
| Dilleniaceae                | 3        | 0        | 3     |
| Melastomataceae             | 3        | 0        | 3     |
| Bignoniaceae                | 1        | 1        | 2     |
| <u>Calophyllum</u> sp.      | 1        | 1        | 2     |
| <u>Guarea</u> sp.           | 0        | 2        | 2     |
| Sapindaceae                 | 0        | 2        | 2     |
| Flacourtiaceae              | 0        | 1        | 1     |
| <u>Perebea</u> sp.          | 0        | 1        | 1     |
| <u>Acacia</u> sp.           | 1        | 0        | 1     |
| Araliaceae                  | 1        | 0        | 1     |
| Burseraceae                 | 1        | 0        | 1     |
| <u>Cephaelis</u> sp.        | 1        | 0        | 1     |
| Elaeocarpaceae              | 1        | 0        | 1     |
| Lecythidaceae               | 1        | 0        | 1     |
| <u>Ouratea</u> sp.          | 1        | 0        | 1     |
| <u>Virola</u> sp.           | 1        | 0        | 1     |
| Unidentified                | 159      | 95       | 254   |

On the newly-created forest edge, canopy openness was similar to that on large gap edges or small light gap centers (pers. obs.). Before edge creation, canopy openness was similar to that reported under closed canopy in undisturbed rain forests (Desmarais and Vázquez 1970). Increased canopy openness is directly related to an increase in duration and intensity of light reaching the forest floor (Chazdon and Fetcher 1984, Chazdon 1986). Thus, light environment on forest edges is probably similar to that found on the edges of large gaps or in the centers of small gaps (Chazdon 1986).

The large number of seeds of light-demanding species that germinated in response to soil disturbance and the germination bioassays confirm that lateral light penetration is adequate to promote seed germination of secondary species along forest edges. Soil disturbance is not a necessary consequence of edge creation, but the disturbed-soil experiment corroborates the importance of soil disturbance in the germination of buried seeds of some secondary species (see also Wesson and Wareing 1969, Bell 1970, Roberts and Feats 1973, Putz 1983). Vázquez-Yanes (1988, pers. comm.) observed that litter removal from the soil surface is enough disturbance to trigger the germination of buried seeds. Other soil variables related with canopy openness may also promote seed germination. Temperature fluctuations (Vázquez-Yanes and Orozco-Segovia 1985) and concomitant changes in soil moisture (Whitmore 1983) have been mentioned as important factors.

Species composition in the soil seed bank study and soil disturbance experiment were similar. Density of germinated

seeds, however, was lower in the soil disturbance experiment. The difference is probably related to higher mortality of seedlings in the field and consequently an underestimation of the total number of germinated seeds in soil disturbance plots. In the soil seed bank study, the soil was spread, watered, and placed in full sun; also seedlings were removed as soon as they were identified and were counted every week. In the soil disturbance plots, the seedlings were not removed and were recorded only after 8 months.

Woody plant density and number of light-demanding species were much higher in the soil disturbance treatment than in the undisturbed soil control. Forest edge plants were mostly of shade-tolerant tree species. Woody light-demanding species, however, were well represented in the soil seed bank. Thus, the low abundance of secondary species in forest edges apparently is related to lack of soil disturbance during edge creation. Differences in the efficiency of uptake of light and the internal use of photosynthate by different species of plants may also have a significant influence on the competitive ability of woody plants following disturbances (Canham and Marks 1985). Even if seedlings of light-demanding species are present during edge creation, they cannot compete with other seedlings if light intensity or other resources are low. Their growth rates are rapid only in proportion to the relative availability of resources (Canham and Marks 1985).

Height growth responses differ between forest edge plants and interior plants. Edge plants grew at twice the rate of

interior plants. Increased growth during the first month following edge creation is probably related to the onset of the rainy season as well as to canopy opening. The rate of emergence of most woody species peaks early in the rainy season (Garwood 1983), and it is during their first 4 weeks that most tropical tree seedlings reach the height permitted by using seed reserves. Afterwards, they grow little in shade, suggesting they are light-limited under the closed canopy (Augsburger 1984). On the forest edge, after one month of edge creation (and germination), the seedlings growth slowed down because the plants were under stress, as evidenced by sun-burned leaves. The increase in light may necessitate physiological acclimation of edge plants to new microenvironmental conditions. Seedlings of shade-tolerant species transferred from full shade to full sunlight showed necrosed leaves and decreased growth rates, possibly because the new environment was too desiccating for seedlings raised in full shade. Seedlings transferred from partial shade to full sunlight did not decrease their growth rates (Fetcher et al. 1987; see also Bazzaz and Carlson 1982, Fletcher et al. 1983). Fletcher et al. (1983, 1987) observed that early successional species were less affected by the previous environment after being moved to a new environment than were late successional species, but the capacity to adjust maximum photosynthetic rate was not related to successional status. Thus, tree species with apparently similar ecological roles do not necessarily have similar acclimation responses. In my study, edge plants were exposed to partial sun,

and between 6-8 months after edge creation their growth rate increased again.

Percent of seedlings surviving the 8-month monitoring period in the forest interior plots was similar to mean annual survivorship under closed forest canopy elsewhere in the neotropics (Uhl 1982, Lieberman and Lieberman 1987), and higher than in the forest edge plots. Lower survivorship on the forest edge seems obviously related to altered microenvironmental conditions such as higher temperature, lower relative humidity, and longer periods of direct sun exposure. During the last monitoring period (6-8 months after edge creation), survivorship was lower and was similar in forest edge and interior. This seems to be related to factors such as increased herbivory--several seedlings were cut--or tree branches falling off, possibly due to heavy rain and winds (pers. obs.).

Lower seedling survivorship on the forest edge was compensated for by higher recruitment rates than in the forest interior. There were two peaks of recruitment during the 8-month observation period. The first one occurred just after edge creation and was probably related to the early rainy season peak in seedling emergence. This is the peak germination season for most species on BCI (Garwood 1983). The second peak of germination occurred in August-September in the middle of the rainy season. During this period seeds of pioneer trees were germinating. A similar peak in germination of pioneer tree species during September-October was reported on BCI (Garwood 1983).

This study demonstrates that edge plants are derived primarily from seedlings and saplings present before the edge was created. These plants may require physiological acclimation to more open conditions before increasing their rate of growth relative to forest interior plants. This research also shows that secondary species are well represented in the soil seed bank when forest edges are created. Germination of some of these species is promoted at the forest edge if the seeds are fully exposed to light. Soil disturbance promotes germination of many buried light-sensitive seeds. However, such disturbance does not normally occur as a result of edge formation in my study area. In cleared forest sites, as disturbance increases in intensity--ranging from single or multiple tree falls, just cutting the forest, cutting and burning, to cutting and bulldozer removal of cut trees and top soil--the vegetation recovery changes from primarily forest trees to successional woody species to forbs and grasses (Uhl 1982, Uhl et al. 1982). Forest edges may reflect, in their species composition and vegetation structure, whether or not they were disturbed when the adjacent clearing was created.

## CHAPTER V EPILOGUE

Although communities are spatially and environmentally heterogeneous, they are usually described on the basis of sample plots in relatively homogeneous areas far from edges (Mueller-Dombois and Ellenberg 1974, Sousa 1984, Pickett and White 1985b, Forman and Godron 1986). Rarely is it appropriate for an ecologist to investigate a forest with an adjacent field and ecotone as a single study site. Methodologically, this is because more samples from heterogeneous areas are required to characterize an ecosystem, and results are less easily compared with other areas or with the same area at another time (Godron and Forman 1983). Also, a good experimental design requires the use of replicable plots, and field-ecotone-forest samples are difficult to replicate (see Hurlbert 1984).

If there is a forest and a contiguous field, then there is an edge. This edge is not necessarily noise or merely a major contribution to experimental error. We cannot just consider edges as anomalies and evade them. It is time to study the non-homogeneous but still important component of the system called edges.

For decades plant ecologists have been busy describing the structure and floristic composition of undisturbed forest or studying secondary successional processes in adjacent fields, i.e. studying "relatively" homogeneous sites that are

characterizable and potentially replicable. Irregular sites and edges have generally been avoided. More recently, forest conservation studies and concerns about the extensive forest fragmentation and deforestation, which are greatly increasing edge extent, have motivated some ecologists to consider edges as an integral part of the forest.

The tropical premontane wet forest edges that I studied are distinctive in terms of vegetation structure and dynamics, although they are composed of the same species present in the forest interior. The mere presence of an adjacent pasture, however, affects the forest edge by modifying its microenvironment. Seedlings and saplings present before the edge was created respond to the new microenvironmental conditions and form a wall of edge vegetation. This edge vegetation isolates the forest from disturbances coming from the pasture. Edge vegetation interferes with lateral light penetration, heated air, or wind coming from the pasture. Although I did not study biotic fluxes, the edge habitat may attract a unique animal community which in turn may influence biotic fluxes such as pollination and seed dispersal.

Contrary to suggestions that forest edges are dominated by secondary species, I found that edges and the forest interior have similar floristic compositions. Secondary tree species are rare despite the fact that the soil from edge sites has many seeds of light-demanding species. Germination of some of these species is promoted at the forest edge when the soil is disturbed and seeds are fully exposed. Disturbance of soil and vegetation

on forest edges, however, is minimal in my study area. This can be attributed to a non-intensive land use due to low human population density, and to cattle being introduced in low numbers only, two years after edge creation. Another important factor is that pastures are not annually burned, as occurs in the lowlands. On the pasture side, disturbance brought about through pasture maintenance and cattle grazing prevents the establishment of secondary successional plants.

This study has documented the significance of edge development to buffering the forest interior from prevalent environmental conditions in the adjacent clearing. It demonstrates that forest canopy removal and soil disturbance affect floristic composition. Type, intensity, and persistence of disturbance determine development of edge vegetation structure and floristic composition on both sides, forest edge and adjacent pasture. The presence of the Kuna Indian Reserve makes my study area unique. Old edges were present because deforestation stopped or will stop at the edge of the Kuna reserve. If we want forest reserves surrounded by buffer zones of primary vegetation, it is important to leave soil and original vegetation undisturbed on their edges.

## REFERENCES

- Andrén H. and P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology* 69:544-547.
- Arias, T. and B. L. Houseal. 1986. The Kuna Yala biosphere comarca. An indigenous application of the conservation concept. Unpublished.
- Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72:777-795.
- Bartholomew, B. 1970. Bare zone between California shrub and grassland communities: the role of animals. *Science* 170:1210-1212.
- Barbour, M. G., J. H. Burk, and W. D. Pitts. 1980. *Terrestrial Plant Ecology*. The Benjamin/Cummings Publishing Company, Inc. Menlo Park, California, USA. 604 p.
- Barton, A. M. 1984. Neotropical pioneer and shade-tolerant tree species: do they partition tree-fall gaps? *Tropical Ecology* 25:196-202.
- Bazzaz, F. A. 1984. Dynamics of wet tropical forests and their species strategies. E. Medina, H. A. Mooney, and C. Vázquez-Yanes (eds.) *Physiological Ecology of Plants of the Wet Tropics*. Dr. W. Junk Publishers. The Hague. The Netherlands. pp:233-243.
- Bazzaz, F. A. and R. W. Carlson. 1982. Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* (Berlin) 54:313-316.
- Becker, P., D. W. Erhart, and A. P. Smith. 1986. *Operator's Manual Canopy Photo Analysis System*. Smithsonian Tropical Research Institute. Unpublished. 61 p.
- Bell, C. R. 1970. Soil distribution and germination experiment. H. T. Odum and R. F. Pigeon (eds.) *A Tropical Rain Forest*. U.S. Atomic Energy Commission, USA. D177-188.
- Belsky, A. J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. *Journal of Ecology* 74:419-437.

- Braun, E. L. 1974. Deciduous Forest of Eastern North America. The Free Press. New York, New York, USA. 596 p.
- Breslin, P. and M. Chapin. 1984. Ecología al estilo Kuna. Desarrollo de Base 8:26-35.
- Brokaw, N. V. L. 1985a. Treefalls, regrowth, and community structure in tropical forests. S. T. A. Pickett and P. S. White (eds.) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press. Orlando, Florida, USA. pp:53-69.
- Brokaw, N. V. L. 1985b. Gap-phase regeneration in a tropical forest. Ecology 66:682-687.
- Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. Journal of Ecology 75:9-19.
- Brown, D. M. 1941. The vegetation of Roan Mountain: a phytosociological and successional study. Ecological Monographs 11:61-97.
- Buell, M. F. and J. E. Cantlon. 1951. A study of two forest stands in Minnesota with an interpretation of the prairie-forest margin. Ecology 32:294-316.
- Burgess, R. L. and D. M. Sharpe. 1981. Introduction. R. L. Burgess and D. M. Sharpe (eds.) Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlag, New York, New York, USA. pp:1-5.
- Canham, C. D. and P. L. Marks. 1985. The response of woody plants to disturbance: patterns of establishment and growth. S. T. A. Pickett and P. S. White (eds.) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press. Orlando, Florida, USA. pp:197-216.
- Chazdon, R. L. 1986. Light variation and carbon gain in rain forest understory palms. Journal of Ecology 74:995-1012.
- Chazdon, R. L. and N. Fetcher. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72:553-564.
- Clark, D. B. 1988. The role of disturbance in the regeneration of neotropical moist forests. K. Bawa and M. Hadley (eds.) Reproductive Ecology of Tropical Forest Plants. UNESCO. In press.
- Clements, F. E. 1936. Nature and structure of the climax. Journal of Ecology 24:252-284.

- Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68:1243-1250.
- Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451-460.
- Curtis, J. T. and R. P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology* 32:476-496.
- Denslow, J. S. 1985. Disturbance-mediated coexistence of species. S. T. A. Pickett and P. S. White (eds.) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press. Orlando, Florida, USA. pp:307-323.
- Desmarais, A. P. and A. Vázquez. 1970. Upper canopy crown closure at El Verde. H. T. Odum and R. F. Pigeon (eds.) *A Tropical Rain Forest*. U.S. Atomic Energy Commission, USA. B-123-133.
- Dickinson, K. J. M. and J. B. Kirkpatrick. 1986. The impact of grazing pressure in clearfelled, burned and undisturbed eucalypt forest. *Vegetatio* 66:133-136.
- Enright, N. 1985. Existence of a soil seed bank under rainforest in New Guinea. *Australian Journal of Ecology* 10:67-71.
- Evans, G. C. 1972. *The Quantitative Analysis of Plant Growth*. University of California Press. Berkeley and Los Angeles, California, USA. 734 p.
- Faber, D., J. N. Karliner, and R. Rice. 1986. Central America: roots of environmental destruction. Green Paper No. 2. Environmental Project on Central America. San Francisco, California, USA. 8 p.
- Fetcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* (Berlin) 58:314-319.
- Fetcher, N., S. F. Oberbauer, G. Rojas, and B. R. Strain. 1987. Efectos del régimen de luz sobre la fotosíntesis y el crecimiento en plántulas de árboles de un bosque lluvioso tropical de Costa Rica. *Revista de Biología Tropical* 35 (Suplemento 1):97-110.
- Forman, R. T. T. 1981. Interaction among landscape elements: a core of landscape ecology. Proceedings of the International Congress organized by the Netherlands Society for Landscape Ecology. Veldhoven, The Netherlands. April 6-11, 1981. pp:35-48.

- Forman, R. T. T. and M. Godron. 1981. Patches and structural components for a landscape ecology. *Bioscience* 31:733-739.
- Forman, R. T. T. and M. Godron. 1986. *Landscape Ecology*. John Wiley and Sons, Inc. New York, New York, USA. 619 pp.
- Foster, R. 1980. Heterogeneity and disturbance in tropical vegetation. M. E. Soulé and B. A. Wilcox (eds.) *Conservation Biology. An Evolutionary-Ecological Perspective*. Sinauer Associates, Inc. Sunderland, Massachusetts, USA. pp:75-92.
- Fritschen, L. J. 1985. Characterization of boundary conditions affecting forest environmental phenomena. B. A. Hutchinson and B. B. Hicks (eds.) *The Forest-Atmosphere Interaction*. D. Reidel Publishing Company. Boston, Massachusetts, USA. pp:3-23.
- Garwood, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* 53:159-181.
- Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- Gleason, H. A. 1926. Concept of plant association. *Bulletin of the Torrey Club* 53:7-26.
- Godron, M. and R. T. T. Forman. 1983. Landscape modification and changing ecological characteristics. H. A. Mooney and M. Godron (eds.) *Disturbance and Ecosystems. Components of Response*. Springer-Verlag. Berlin, Germany. pp:12-28.
- Gordon, D. T. 1973. Damage from wind and other causes in mixed fir-red fir stands adjacent to clearcuttings. *USDA Forest Service Research Paper PSW-90*, USA. 22 p.
- Grime, J. J. 1979. *Plant Strategies and Vegetation Processes*. John Wiley and Sons. Bath, England. 222 p.
- Grimm, E. C. 1984. Fire and other factors controlling the big woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* 54:291-311.
- Grubb, P. J. 1985. Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. J. White (ed.) *The Population Structure of Vegetation*. Dr. W. Junk Publishers. Dordrecht, The Netherlands. pp:595-621.

- Grubb, P. J., R. J. Lloyd, T. D. Pennington, and T. C. Whitmore. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. *Journal of Ecology* 51:567-601.
- Grubb, P. J. and T. C. Whitmore. 1966. A comparison of montane and lowland rain forest in Ecuador. II. The climate and its effects on the distribution and physiognomy of the forests. *Journal of Ecology* 54:303-333.
- Guevara, S. S. and A. Gómez-Pompa. 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. *Journal of Arnold Arboretum* 53:312-335.
- Gysel, L. W. 1951. Borders and openings of beech-maple woodlands in southern Michigan. *Journal of Forestry* 49:13-19.
- Harmon, M. E. 1982. Decomposition of standing dead trees in the Southern Appalachian Mountains. *Oecologia (Berlin)* 52:214-215.
- Harper, J. L. 1977. *Population Biology of Plants*. Academic Press. London, England. 892 p.
- Harris, L. D. and J. D. McElveen. 1981. Effect of forest edges on North Florida breeding birds. *IMPAC Report* 6:1-23.
- Hibbs, D. E. 1982. Gap dynamics in a hemlock-hardwood forest. *Canadian Journal of Forest Research* 12:522-527.
- Hopkins, M. S. and A. W. Graham. 1983. The species composition of soil seed banks beneath lowland tropical forest in North Queensland, Australia. *Biotropica* 15:90-99.
- Hubbell, S. P. and R. B. Foster. 1987. La estructura espacial en gran escala de un bosque neotropical. *Revista de Biología Tropical* 35 (Suplemento 1):7-22.
- Hubbell, S. P. and R. B. Foster. 1988. Canopy gaps and the dynamics of a neotropical forest. M. J. Crawley (ed.) *Plant Ecology*. Blackwell Scientific. Oxford, England. pp:77-96.
- Huber, R. 1986. Kuna Indians move to preserve rain-forest. *Naturalist* 6:12-17.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187-211.
- Jenny, H. 1961. Derivation of state factor equations of soil and ecosystems. *Soil Science Society Proceedings*. pp:385-388.

- Johnston, V. R. 1947. Breeding birds of the forest edge in Illinois. *Condor* 49:45-53.
- Lal, R. 1987. Tropical Ecology and Physical Edaphology. John Wiley and Sons. New York, New York, USA. 732 p.
- Lang, G. E. and D. H. Knight. 1979. Decay rates for boles of tropical trees in Panama. *Biotropica* 11:316-317.
- Lawson, G. W., K. O. Armstrong-Mensah, and J. B. Hall. 1970. A catena in tropical moist semi-deciduous forest near Kade, Ghana. *Journal of Ecology* 58:371-398.
- Lawson, T. L., R. Lal, and K. Oduro-Afriyie. 1981. Rainfall redistribution and microclimatic changes over a cleared watershed. R. Lal and E. W. Russell (eds.) *Tropical Agricultural Hydrology*. John Wiley and Sons. New York, New York, USA. pp:141-151.
- Lawton, R. O. and F. E. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical lower montane rain forest. *Ecology* 69:764-777.
- Lebrón, M. L. 1979. An autoecological study of Palicourea riparia Benthham as related to rain forest disturbance in Puerto Rico. *Oecologia (Berlin)* 42:31-46.
- Lee, R. 1978. Forest Microclimatology. Columbia University Press. New York, New York, USA. 276 p.
- Leopold, A. 1933. Game Management. Charles Scribner's Sons. New York, New York, USA. 481 p.
- Levenson, J. B. 1981. Woodlots as biogeographic islands in Southeastern Wisconsin. R. L. Burgess and D. M. Sharpe (eds.) *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag. New York, New York, USA. pp:13-39.
- Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Science. USA.* 71:2744-2747.
- Lieberman, D. and M. Lieberman. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *Journal of Tropical Ecology* 3:347-358.
- Liew, T. C. and Wong F. O. 1973. Density, recruitment, mortality and growth of Dipterocarp seedlings in virgin and logged-over forests in Sabah. *The Malaysian Forester* 36:3-15.
- Longman, K. A. and J. Jenik. 1974. Tropical Forest and its Environment. Lowe and Brydone (Printers) Ltd, Thetford, Norfolk, UK. 196 p.

- Lovejoy, T. E., R. O. Bierregaard, J. M. Rankin, and H. O. Schubart. 1983. Ecological dynamics of tropical forest fragments. S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (eds.) Tropical Rain Forest: Ecology and Management. Blackwell Scientific Publications. Oxford, England. pp:377-384.
- Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard, K. S. Brown, L. H. Emmons, and M. E. Van der Voort. 1984. Ecosystem decay of Amazon forest remnants. M. H. Nitecki (ed.) Extinctions. The University of Chicago Press. Chicago, Illinois, USA. pp:295-325.
- Lovejoy, T. E., R. O. Bierregaard, Jr., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. M. E. Soulé (ed.) Conservation Biology: Science of Diversity. Sinauer. Sunderland, Massachusetts, USA. pp:257-285.
- Lowrance, R., R. Todd, J. Fail, Jr., O. Hendrickson, Jr., R. Leonard, L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. Bioscience 34:374-377.
- Margalef, R. 1978. Perspectivas de la Teoría Ecológica. Editorial Blume. Barcelona, Spain. 110 p.
- McCoy, E. D., S. S. Bell, and K. Walters. 1986. Identifying biotic boundaries along environmental gradients. Ecology 67:749-759.
- McDiarmid, R. W., R. E. Ricklefs, and M. S. Foster. 1977. Dispersal of Stemmademia donnell-smithii (Apocynaceae) by birds. Biotropica 9:9-25.
- Maser C. and J. M. Trappe (tech. eds.) 1984. The Seen and Unseen World of the Fallen Tree. General Technical Report PNW-164. Portland, Oregon. U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, USA. 56 pp.
- Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. American Naturalist 120:533-536.
- Miller, D. R. and J. D. Lin. 1985. Canopy architecture of a red maple edge stand measured by a point drop method. B. A. Hutchinson and B. B. Hicks (eds.) The Forest-Atmosphere Interaction. D. Keidel Publishing Company. Boston, Massachusetts, USA. pp:59-70.

- Mooney, H. A. and M. Godron (eds.). 1983a. Disturbance and Ecosystems. Components of Response. Springer-Verlag. Berlin, Germany. 292 p.
- Mooney, H. A. and M. Godron. 1983b. Preface. H. A. Mooney and M. Godron (eds.) Disturbance and Ecosystems. Components of Response. Springer-Verlag. Berlin, Germany. pp:v-vi.
- Muller, C. H. and W. H. Muller. 1964. Antibiosis as a factor in vegetation patterns. Science 144:889-890.
- Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons. New York, New York, USA. 547 p.
- Myers, N. 1981. The hamburger connection: how Central America's forests become North America's hamburgers. Ambio 10:3-8.
- Noss, R. F. 1983. A regional landscape approach to maintain diversity. Bioscience 33:700-706.
- Odum, H. T. 1983. Systems Ecology: an Introduction. John Wiley and Sons. New York, New York, USA. 644 p.
- Oldeman, R. A. A. 1986. On the limits of forest ecosystems: do they have skins? Proceedings 18th. IUFRO World Congress, Division 6. Ljubljana, Yugoslavia. pp:312-324.
- Parsons, J. J. 1976. Forest to pasture: development or destruction? Revista de Biologia Tropical 24:121-138.
- PEMASKY. 1985. Proyecto de estudio para el manejo de areas silvestres de Kuna Yala. PEMASKY booklet. Panama, Panama. 2 p.
- Petersen, R. G. 1985. Design and Analysis of Experiments. Marcel Dekker, Inc. New York, New York, USA. 429 p.
- Petranka, J. W. and J. K. McPherson. 1979. The role of Rhus copallina in the dynamics of the forest-prairie ecotone in North Central Oklahoma. Ecology 60:956-965.
- Pickett, S. T. A. and P. S. White (eds.) 1985a. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Inc. Orlando, Florida, USA. 472 p.
- Pickett, S. T. A. and P. S. White. 1985b. Patch dynamics: a synthesis. S. T. A. Pickett and P. S. White (eds.) The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Inc. Orlando, Florida, USA. pp:371-384.

- Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* 64:1069-1074.
- Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713-1724.
- Putz, F. E. and K. Milton. 1982. Tree mortality rates on Barro Colorado Island. E. G. Leigh, A. S. Rand, and D. W. Windsor (eds.) *The Ecology of a Tropical Forest*. Smithsonian Institution Press. Washington, D. C., USA. pp:95-100.
- Ranney, J. W. 1977. Forest Island Edges--their structure, development, and importance to regional forest ecosystem dynamics. Oak Ridge National Laboratory. Environmental Sciences Division. Publication No. 1069. 36 p.
- Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. R. L. Burgess and D. M. Sharpe (eds.) *Forest Island Dynamics in Man-Dominated Landscapes*. Springer-Verlag. New York, New York, USA. pp:67-95.
- Raynor, G. S. 1969. Wind and temperature structure in a coniferous forest and a contiguous field. *Forest Science* 17:351-363.
- Reiners, W. A. 1983. Disturbance and basic properties of ecosystem energetics. H. A. Mooney and M. Godron (eds.) *Disturbance and Ecosystems. Components of Response*. Springer-Verlag. Berlin, Germany. pp:83-98.
- Ricklefs, R. E. 1979. *Ecology*. Chiron Press, Inc. Concord, Massachusetts, USA. 966 p.
- Risser, P. G., J. R. Karr, and R. T. T. Forman. 1984. *Landscape Ecology: Directions and Approaches*. Special Publication 2. Illinois Natural History Survey. Champaign, Illinois, USA. 18 p.
- Roberts, E. H. and P. W. Feast. 1973. Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. *Journal of Applied Ecology* 10:133-143.
- Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology*:63:1533-1546.
- SAS. 1984. *SAS/ETS User's Guide, Version 5 Edition*. SAS Institute Inc. Cary, North Carolina, USA. 738 p.

- Schulz, J. P. 1960. Ecological studies on rain forest in northern Suriname. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen. Afd. Natuurkunde: Tweede Reeks* 53:1-267.
- Shipley, B. and P. A. Keddy. 1987. The individualistic and community-unit concepts as falsifiable hypotheses. *Vegetatio* 69:47-55.
- Small, M. F. and M. L. Hunter. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* (Berlin) 76:62-64.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Soulé, M. E. 1986. The effects of fragmentation. M. E. Soulé (ed.) *Conservation Biology: Science of Diversity*. Sinauer, Sunderland, Massachusetts, USA. pp:233-236.
- Sprugel, D. G. 1976. Dynamics structure of wave-regenerated Abies balsamea forests in the North-Eastern United States. *Journal of Ecology* 64:889-910.
- Sprugel, D. G. and F. H. Bormann. 1981. Natural disturbance and the steady state in high-altitude balsam fir forests. *Science* 211:390-393.
- Stanton, M. L. 1983 Spatial patterns in the plant community and their effects upon insect search. S. Ahmad (ed.) *Herbivorous Insects*. Academic Press. New York, New York, USA. pp:125-157.
- Thompson, O. E. and R. T. Pinker. 1975. Wind and temperature profile characteristics in a tropical evergreen forest in Thailand. *Tellus* 6:562-573.
- Thompson, J. N. and M. F. Willson. 1978. Disturbance and the dispersal of fleshy fruits. *Science* 200:1161-1163.
- Tosi, J. A., Jr. 1971. *Zonas de vida en la República de Panamá*. FAO. Rome, Italy. 89 pp.
- Trimble, G. R. and E. H. Tryon. 1966. Crown encroachment into openings cut in Appalachian hardwood stands. *Journal of Forestry* 62:104-108.
- Tryon, E. H. and G. R. Trimble. 1969. Effect of distance from stand border on height of hardwood reproduction in openings. *West Virginia Academy of Sciences* 41:125-133.

- Uhl, C. 1982. Recovery following disturbances of different intensities in the Amazon rain forest of Venezuela. *Interiencia* 7:19-24.
- Uhl, C., C. Jordan, K. Clark, H. Clark, and R. Herrera. 1982. Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatments. *Oikos* 38:313-320.
- Uhl, C. and R. Buschbacher. 1985. A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the eastern Amazon. *Biotropica* 17:265-268.
- UNESCO. 1978. Tropical Forest Ecosystems: a State of Knowledge Report. UNESCO. Paris, France. 683 p.
- Vázquez-Yanes, C. 1980. Notas sobre la autoecología de los árboles pioneros de rápido crecimiento de la selva tropical lluviosa. *Tropical Ecology* 21:103-111.
- Vázquez-Yanes, C. and H. Smith. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer trees Cecropia obtusifolia and Piper auritum and its ecological significance. *New Phytologist* 92:477-485.
- Vázquez-Yanes, C. and A. Orozco-Segovia. 1985. Posibles efectos del microclima de los claros de la selva, sobre la germinación de tres especies de árboles pioneros: Cecropia obtusifolia, Heliocarpus donnell-smithii y Piper auritum. A. Gómez-Pompa y S. Del Amo R. (eds.) Investigaciones sobre la Regeneración de Selvas Altas en Veracruz, México II. INIREB. Editorial Alhambra Mexicana, S.A. de C.V. México, México. pp:241-253.
- Verner, J., M. L. Morrison, and C. J. Ralph (eds) 1986. Wildlife 2000. Modeling Habitat Relationships of Terrestrial Vertebrates. The University of Wisconsin Press, Ltd. Madison, Wisconsin, USA. 470 p.
- Wales, B. A. 1972. Vegetation analysis of northern and southern edges in a mature oak-hickory forest. *Ecological Monographs* 42:451-471.
- Waring, R. H. 1987. Characteristics of trees predisposed to die. *Bioscience* 37:569-574.
- Waser, N. M. and M. V. Price. 1981. Effects of grazing on diversity of annual plants in the Sonoran Desert. *Oecologia* (Berlin) 50:407-411.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-22.

- Wells, P. V. 1964. Antibiosis as a factor in vegetation patterns. *Science* 144:889.
- Wesson, G. and P. Wareing. 1969. The role of light in germination of naturally occurring populations of buried weed seeds. *Journal of Experimental Botany* 20:403-413.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229-299.
- White, P. S. and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. S. T. A. Pickett and P. S. White (eds.) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press. Orlando, Florida, USA. pp:3-13.
- Whitmore, T. C. 1975. *Tropical Rain Forests of the Far East*. Clarendon Press. Oxford, England. 282 p.
- Whitmore, T. C. 1983. Secondary succession from seed in tropical rain forests. *Forestry Abstracts* 44:767-779.
- Whittaker, R. H. 1963. Net production of heath balds and forest heaths in the Great Smoky Mountains. *Ecology* 44:176-182.
- Whittaker, R. H. 1975. *Communities and Ecosystems*. MacMillan Publishing Company. New York, New York, USA. 385 p.
- Whittaker, R. H. and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12:117-139.
- Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421-427.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. M. E. Soulé (ed.) *Conservation Biology: Science of Diversity*. Sinauer, Sunderland, Massachusetts, USA. pp:237-256.
- Wilkinson, L. 1986. *SYSTAT: The System for Statistics*. Systat Inc. Evanston, Illinois, USA.

## APPENDIX A

### TOPOGRAPHY AND ASPECT OF THE STUDY SITES

## 0.8-YEAR-OLD SITE

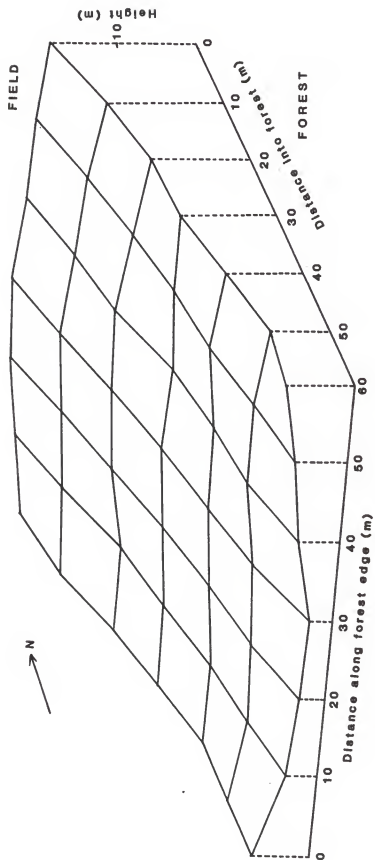


Figure A-1. Topography and aspect of the 0.8-year-old study site.

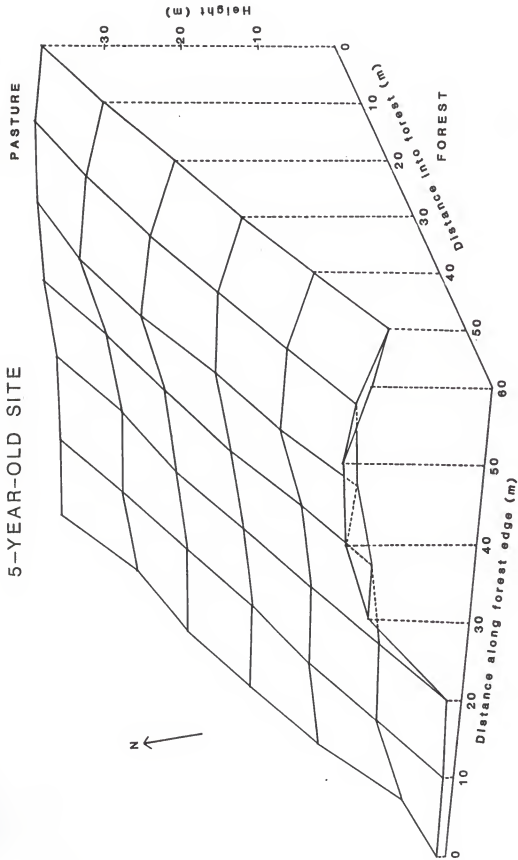


Figure A-2. Topography and aspect of the 5-year-old study site.

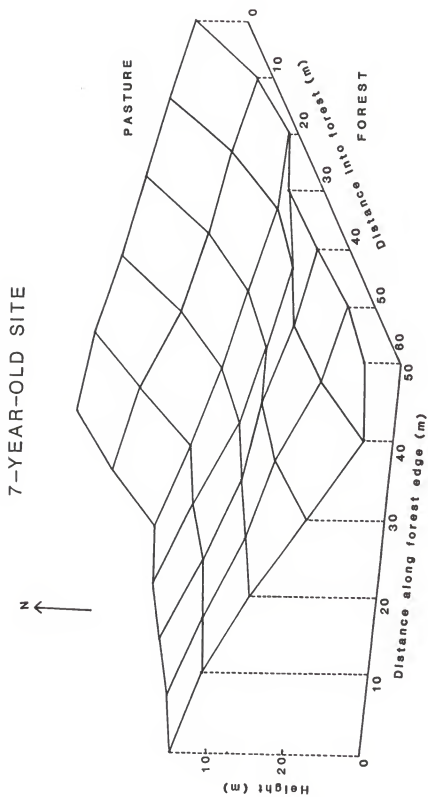


Figure A-3. Topography and aspect of the 7-year-old study site.

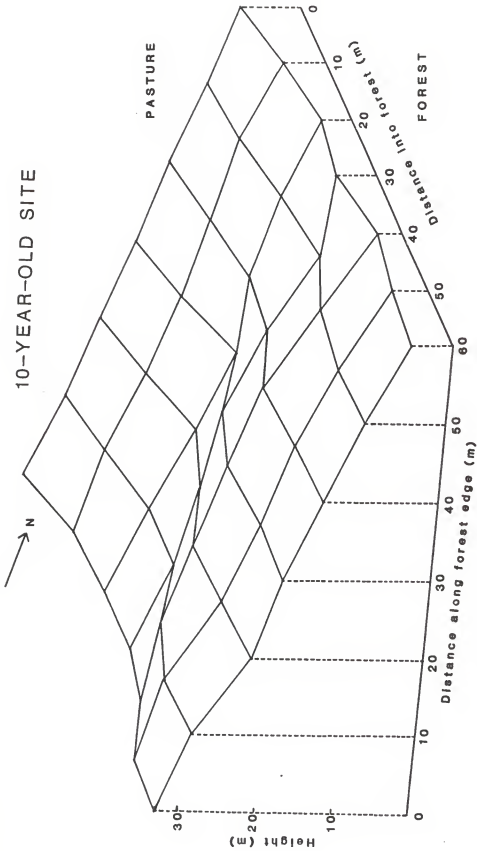


Figure A-4. Topography and aspect of the 10-year-old study site.

## 12-YEAR-OLD SITE

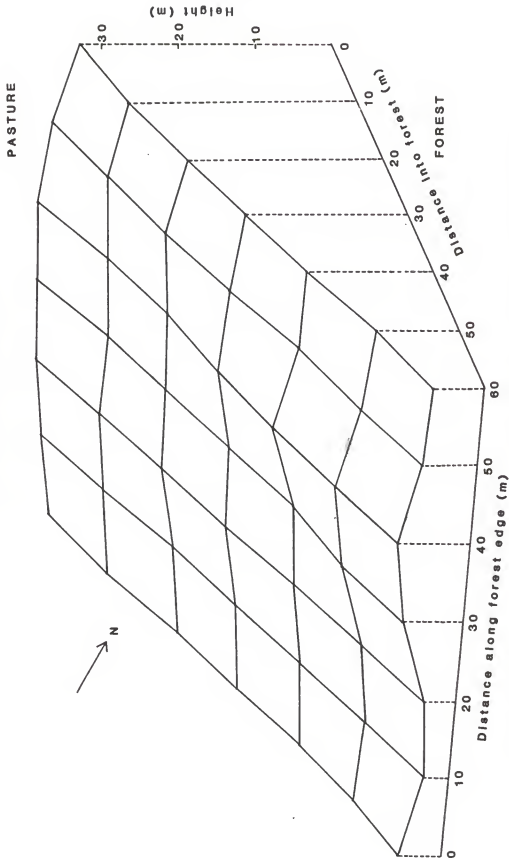


Figure A-5. Topography and aspect of the 12-year-old study site.

## APPENDIX B

SOIL ANALYSES PROCEDURES AND PHYSICAL AND CHEMICAL RESULTS

## SOIL PHYSICAL AND CHEMICAL ANALYSES PROCEDURES

The soil samples were air dried and sent to the Soils Department of the Instituto de Investigaciones Agropecuarias de Panamá (IDIAP) to be analyzed for physical and chemical properties. Texture was determined using the Bouyoucos hydrometer method, pH was measured in a soil-water mixture of 1:2, and organic matter was analyzed using the Walkley-Black method. Phosphorus, K, Ca and Mg were extracted with double-acid solution. Aluminum was extracted with KCl. Calcium, Mg and Al were measured by atomic absorption. Phosphorus and K were analyzed by spectroscopy (IDIAP, pers. comm.).

Table B-1. Physical and chemical properties of forest interior soil samples in the study sites. Values are means of two samples ( $\pm$  sd). Means in the same column accompanied by a superscript are significantly different at  $\alpha = 0.05$  (one-way ANOVA).

| Depth<br>(cm) | Edge age<br>(yr) | Texture (%) |      |      | pH  | OM<br>(%)  | P<br>mg/kg |
|---------------|------------------|-------------|------|------|-----|------------|------------|
|               |                  | Sand        | Silt | Clay |     |            |            |
| 0-10          | 0.8              | 51          | 31   | 18   | 4.1 | 6.94(0.22) | 4.3(0.4)   |
|               | 5                | 42          | 33   | 25   | 4.4 | 5.06(2.42) | 3.4(1.6)   |
|               | 7                | 54          | 26   | 20   | 4.6 | 7.44(1.42) | 3.4(0.8)   |
|               | 10               | 34          | 40   | 26   | 4.2 | 7.62(0.98) | 3.2(0.4)   |
|               | 12               | 46          | 29   | 25   | 4.3 | 7.38(0.97) | 3.2(0.4)   |
|               | New edge         | 45          | 27   | 28   | 4.9 | 6.10(0.28) | 2.9(0.0)   |
| 10-30         | 0.8              | 40          | 30   | 30   | 4.4 | 2.82(0.19) | 4.1(2.5)   |
|               | 5                | 36          | 25   | 39   | 4.6 | 2.64(1.08) | 2.0(0.4)   |
|               | 7                | 37          | 28   | 35   | 4.6 | 2.62(0.47) | 2.3(0.8)   |
|               | 10               | 21          | 40   | 39   | 4.3 | 2.18(0.62) | 2.0(0.4)   |
|               | 12               | 28          | 28   | 44   | 4.5 | 3.02(1.80) | 2.0(0.4)   |
|               | New edge         | 41          | 26   | 33   | 4.6 | 3.02(0.90) | 1.7(0.0)   |

Table B-1--extended.

| K<br>mg/kg | Ca<br>meq/100g | Mg<br>meq/100g | Al<br>meq/100g |
|------------|----------------|----------------|----------------|
| 89 (9)     | 1.1(0.1) b     | 1.8(0.1) b     | 4.8(0.6) a     |
| 92(36)     | 1.2(0.2) b     | 1.6(0.4) b     | 2.2(0.6) b     |
| 128(33)    | 1.4(0.4) b     | 2.0(0.1) b     | 3.2(1.1) ab    |
| 83 (4)     | 0.7(0.1) b     | 1.5(0.3) b     | 3.1(0.7) ab    |
| 60 (4)     | 1.1(0.1) b     | 2.1(0.6) b     | 2.2(0.3) b     |
| 44(13)     | 4.0(1.2) a     | 4.2(1.2) a     | 0.4(0.3) c     |
| 52 (0)     | 0.8(0.0)       | 0.8(0.3) b     | 6.1(0.1) ab    |
| 59(12)     | 0.9(0.1)       | 0.9(0.4) b     | 3.2(0.8) bc    |
| 66(16)     | 0.7(0.1)       | 1.6(0.1) b     | 4.7(1.8) ab    |
| 62(23)     | 0.6(0.0)       | 1.2(0.1) b     | 3.6(0.3) b     |
| 33(11)     | 0.7(0.1)       | 1.8(0.8) b     | 2.9(0.1) bc    |
| 19 (1)     | 1.8(0.8)       | 2.9(0.6) a     | 1.2(0.8) c     |

Table B-2. Physical and chemical properties of forest interior, pasture-forest border, and pasture soil samples. Values are means of four samples ( $\pm$  sd) from the 5- and 12-year-old sites.

| Depth<br>(cm) | Location | Texture (%) |      |      | pH  | OM<br>(%)  | P<br>mg/kg |
|---------------|----------|-------------|------|------|-----|------------|------------|
|               |          | Sand        | Silt | Clay |     |            |            |
| 0-10          | Forest   | 44          | 31   | 25   | 4.4 | 6.22(2.02) | 3.3(0.1)   |
|               | Border   | 50          | 25   | 27   | 4.4 | 8.54(1.75) | 3.4(0.4)   |
|               | Pasture  | 51          | 28   | 22   | 4.8 | 7.67(1.00) | 3.1(0.6)   |
| 10-30         | Forest   | 32          | 27   | 42   | 4.5 | 2.83(1.23) | 2.0(0.3)   |
|               | Border   | 37          | 29   | 35   | 4.3 | 4.15(1.47) | 2.6(0.7)   |
|               | Pasture  | 29          | 26   | 46   | 4.5 | 2.86(0.80) | 3.2(1.8)   |

Table B-2--extended.

| K<br>mg/kg | Ca<br>meq/100g | Mg<br>meq/100g | Al<br>meq/100g |
|------------|----------------|----------------|----------------|
| 76(28)     | 1.1(0.2)       | 1.8(0.5)       | 2.2(0.4)       |
| 137(48)    | 1.4(0.3)       | 1.4(0.3)       | 2.3(1.0)       |
| 99(37)     | 2.3(1.0)       | 2.3(1.0)       | 1.1(0.6)       |
| 46(18)     | 0.8(0.2)       | 0.8(0.2)       | 3.0(0.4)       |
| 93(37)     | 0.9(0.1)       | 0.9(0.1)       | 2.8(1.0)       |
| 78(44)     | 1.0(0.2)       | 1.0(0.2)       | 2.5(0.5)       |

APPENDIX C

MEAN MAXIMUM AND MINIMUM TEMPERATURES AND RELATIVE HUMIDITY  
ALONG TRANSECTS GOING FROM PASTURE TO FOREST INTERIOR  
IN THE STUDY SITES

Table C-1. Mean maximum temperatures along transects extending from 25 m into the pasture to 45 m into the forest. Values in parentheses are standard errors. For edge 0.8, 5, 10, and 12 years old, n=7, for edge 7 years old, n=6.

| Edge age<br>(yr) | Pasture       |               |               | Distance (m)<br>Border |               |               | Forest        |               |               |
|------------------|---------------|---------------|---------------|------------------------|---------------|---------------|---------------|---------------|---------------|
|                  | 25            | 15            | 5             | 0                      | 5             | 15            | 25            | 35            | 45            |
| 0.8              | 27.6<br>(0.5) | 28.1<br>(0.5) | 27.4<br>(0.3) | 26.5<br>(0.3)          | 26.0<br>(0.2) | 26.4<br>(0.3) | 25.3<br>(0.2) | 25.7<br>(0.2) | 25.3<br>(0.2) |
| 5                | 30.1<br>(0.6) | 29.6<br>(0.6) | 28.8<br>(0.5) | 27.8<br>(0.4)          | 27.4<br>(0.3) | 27.4<br>(0.3) | 27.4<br>(0.4) | 27.5<br>(0.3) | 27.3<br>(0.4) |
| 7                | 26.3<br>(0.2) | 26.5<br>(0.4) | 26.1<br>(0.2) | 26.1<br>(0.2)          | 25.6<br>(0.2) | 25.0<br>(0.3) | 25.1<br>(0.2) | 25.0<br>(0.1) | 25.5<br>(0.1) |
| 10               | 27.5<br>(0.3) | 27.8<br>(0.4) | 27.4<br>(0.4) | 27.4<br>(0.4)          | 25.7<br>(0.3) | 25.1<br>(0.3) | 24.9<br>(0.2) | 25.4<br>(0.3) | 25.5<br>(0.2) |
| 12               | 28.2<br>(0.4) | 27.9<br>(0.4) | 27.5<br>(0.3) | 26.3<br>(0.2)          | 25.8<br>(0.2) | 25.6<br>(0.2) | 25.2<br>(0.1) | 25.5<br>(0.2) | 25.1<br>(0.2) |

Table C-2. Mean minimum temperatures along gradients extending from 25 m into the pasture to 45 m into the forest. Values in parentheses are standard errors. For edge 0.8, 5, 10, and 12 years old, n=7, for edge 7 years old, n=6.

| Edge age<br>(yr) | Pasture       |               | 5             | Distance (m)<br>Border |               |               | Forest        |               |               |
|------------------|---------------|---------------|---------------|------------------------|---------------|---------------|---------------|---------------|---------------|
|                  | 25            | 15            |               | 0                      | 5             | 15            | 25            | 35            | 45            |
| 0.8              | 22.7<br>(0.4) | 22.9<br>(0.3) | 22.4<br>(0.2) | 22.4<br>(0.2)          | 22.3<br>(0.2) | 22.9<br>(0.2) | 22.4<br>(0.2) | 22.7<br>(0.2) | 22.5<br>(0.2) |
| 5                | 23.1<br>(0.4) | 22.3<br>(0.4) | 22.4<br>(0.5) | 22.4<br>(0.5)          | 22.5<br>(0.3) | 22.5<br>(0.3) | 22.4<br>(0.3) | 22.7<br>(0.4) | 22.1<br>(0.4) |
| 7                | 22.7<br>(0.4) | 23.2<br>(0.3) | 22.5<br>(0.2) | 22.6<br>(0.3)          | 22.2<br>(0.3) | 22.0<br>(0.2) | 21.9<br>(0.3) | 21.8<br>(0.3) | 21.8<br>(0.3) |
| 10               | 21.8<br>(0.3) | 22.6<br>(0.2) | 22.2<br>(0.2) | 22.1<br>(0.3)          | 22.1<br>(0.3) | 21.9<br>(0.3) | 21.9<br>(0.3) | 21.8<br>(0.3) | 21.8<br>(0.3) |
| 12               | 22.6<br>(0.3) | 21.9<br>(0.3) | 21.7<br>(0.3) | 21.6<br>(0.3)          | 21.6<br>(0.3) | 21.7<br>(0.3) | 21.6<br>(0.3) | 22.0<br>(0.3) | 21.6<br>(0.3) |

Table C-3. Mean relative humidity percent along transects extending from 25 m into the pasture to 45 m into the forest. Values in parentheses are standard errors. For edge 0.8 years old, n=7, for edge 5, 7, 10 and 12 years old, n=6.

| Edge age<br>(yr) | Pasture       |               |               | Distance (m)<br>Border |               |               | Forest        |               |               |
|------------------|---------------|---------------|---------------|------------------------|---------------|---------------|---------------|---------------|---------------|
|                  | 25            | 15            | 5             | 0                      | 5             | 15            | 25            | 35            | 45            |
| 0.8              | 85.3<br>(2.2) | 85.9<br>(3.1) | 87.3<br>(3.5) | 88.0<br>(2.7)          | 89.3<br>(2.0) | 91.0<br>(2.0) | 91.3<br>(1.8) | 91.3<br>(2.2) | 91.9<br>(2.1) |
| 5                | 76.0<br>(2.7) | 74.2<br>(3.8) | 75.2<br>(3.1) | 78.0<br>(3.2)          | 79.5<br>(3.5) | 82.3<br>(2.4) | 83.8<br>(2.4) | 84.3<br>(2.3) | 85.0<br>(2.4) |
| 7                | 84.5<br>(2.5) | 86.0<br>(2.9) | 86.0<br>(2.0) | 86.7<br>(2.3)          | 88.5<br>(2.8) | 89.2<br>(2.3) | 90.2<br>(1.9) | 89.2<br>(2.5) | 89.7<br>(2.4) |
| 10               | 81.0<br>(4.2) | 81.5<br>(4.1) | 83.0<br>(4.2) | 85.7<br>(3.3)          | 87.8<br>(2.4) | 88.5<br>(2.5) | 89.7<br>(2.5) | 86.5<br>(3.1) | 86.3<br>(3.1) |
| 12               | 82.7<br>(1.9) | 82.2<br>(2.1) | 82.5<br>(1.7) | 84.5<br>(2.5)          | 87.0<br>(1.9) | 88.7<br>(1.8) | 88.5<br>(2.3) | 89.5<br>(2.2) | 89.8<br>(1.3) |

## BIOGRAPHICAL SKETCH

Guadalupe was born in Xalapa, Veracruz, Mexico. She attended the University of Veracruz in Orizaba and obtained her bachelors degree in agricultural chemistry in 1978, with a thesis entitled "Determination of the Phenotypic Segregations and Biochemical Variations in Opaque-2 Segregants of Tropical Varieties of Corn." She traveled for several months in Europe and Mexico and in 1979 discovered ecology. She pursued a masters degree in ecology and biotic resource management at the Instituto Nacional de Investigaciones sobre Recursos Bióticos in Xalapa, Veracruz. She obtained her Master of Science in 1982 with a thesis entitled "Biomass and Nutrient Content in the Vegetation and Soil of Two Secondary Successional Stages of Tropical Wet Forest." She expects to go back to Mexico in 1989 and do research on plant community ecology.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Francis E. Putz  
Francis E. Putz, Chairperson  
Associate Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Walter S. Judd  
Walter S. Judd  
Associate Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Hugh Popenoe  
Hugh Popenoe  
Professor of Soil Science

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Kenneth L. Buhr  
Kenneth L. Buhr  
Assistant Professor of Agronomy

This dissertation was submitted to the Graduate Faculty of the Department of Botany in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1989

\_\_\_\_\_  
Dean, Graduate School